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REVISION OF THE MILLIPED FAMILY EURYMERODESMIDAE  
(POLYDESMIDA: CHELODESMIDEA)

BY

ROWLAND M. SHELLEY

North Carolina State Museum of Natural Science  
P.O. Box 27647, Raleigh, North Carolina 27611

ABSTRACT — *Eurymerodesmus* Brolemann, the sole genus in the chelodesmoid milliped family Eurymerodesmidae, is a speciose mosaic complex that covers a substantial part of the central, south-central, and southeastern United States. It is the dominant polydesmoid in prairie ecosystems, and forms occur in diverse biotopes in both mesic and arid environments. Autapomorphies include a ventral mandibular ridge and medial projection in both sexes; elaborate, hirsute gonopodal apertures; laterally oriented gonopods; simple, unmodified telopodites; and long, silken prefemoral hairs. *Eurymerodesmus* contains 25 species, five of which, *elevatus*, *caesariatus*, *crassatus*, *dactylocyphus*, and *clavatus*, are newly described. *Kewanius* and *Paresmus*, both authored by Chamberlin, are placed in the generic synonymy, and the following species-group names are assigned to specific synonymies: *Paresmus columbus* Causey; *E. bentonus*, *plishneri*, *spectabilis*, and *wellesleybentoni*, all by Causey; *creolus* and *schmidti*, both by Chamberlin; and *hamatilis* and *minimus*, both by Loomis. *Eurymerodesmus booneus* Chamberlin is a synonym of *Auturus evides* (Bollman). *Eurymerodesmus christianus* and *louisianus*, both by Chamberlin, are reduced to subspecies of *E. varius* (McNeill); *E. planus* Causey is a race of *E. birdi* Chamberlin. The genus is divided into four lineages, three of which, the *hispidipes*, *birdi*, and *melacis* lines, are composed of one species group each; the *Kewanius* lineage is comprised of four species groups. Relationships among the lineages are *melacis* + (*hispidipes* + (*birdi* + *Kewanius*)). Along with *Sigmoria*, *Eurymerodesmus* directs attention to the evolutionary dynamics of mosaic complexes in the Diplopoda and their potential utility as new investigative subjects that may hold more inherent appeal to other biologists than traditional milliped taxonomy.

INTRODUCTION

The central, south-central, and southeastern United States — from northeastern Nebraska, central Illinois, and southeastern North Carolina to the Rio Grande and north Florida (Fig. 1) — is home to

the Eurymerodesmidae (Polydesmida: Chelodesmidea). Sympatric through much of this area with eastern Nearctic components of the chelodesmoid families Xystodesmidae and Platyrhacidae, some of whose species they superficially resemble in external body form, eurymerodesmids inhabit a diversity of biotopes including mesic deciduous forest litter in Illinois, the Ozark Plateau, and the Ouachita Physiographic Province; under logs in xeric, sandy, southeastern environments; and under logs and dung in grasslands of the Central Plains. They are the dominant polydesmoid diplopods in prairie ecosystems, ranging westward onto the Edwards Plateau and across the Pecos River in central and southern Texas.

The Eurymerodesmidae is one of the best defined chelodesmoid families, but its affinities within the suborder are obscure. Autapomorphies include a ventral ridge along the mandibular stipes in both sexes that extends into a medial projection, usually larger in males; laterally oriented gonopods with the cannulas located ventrolaterad on the coxa instead of mediad; simple, unmodified, and caudally, instead of anteriorly, projecting telopodites; highly modified and variable gonopodal apertures with relatively unmodified, simple gonopods, instead of vice versa; a variably hirsute aperture indented anteromediad, instead of glabrous and not indented; and extremely long, silken prefemoral hairs, in some forms nearly half as long as the telopodite, extending in variable numbers and arrangements along the stem of the structure, rather than short hairs chiefly restricted to the basal region. The most striking features of eurymerodesmids are the variable aper-

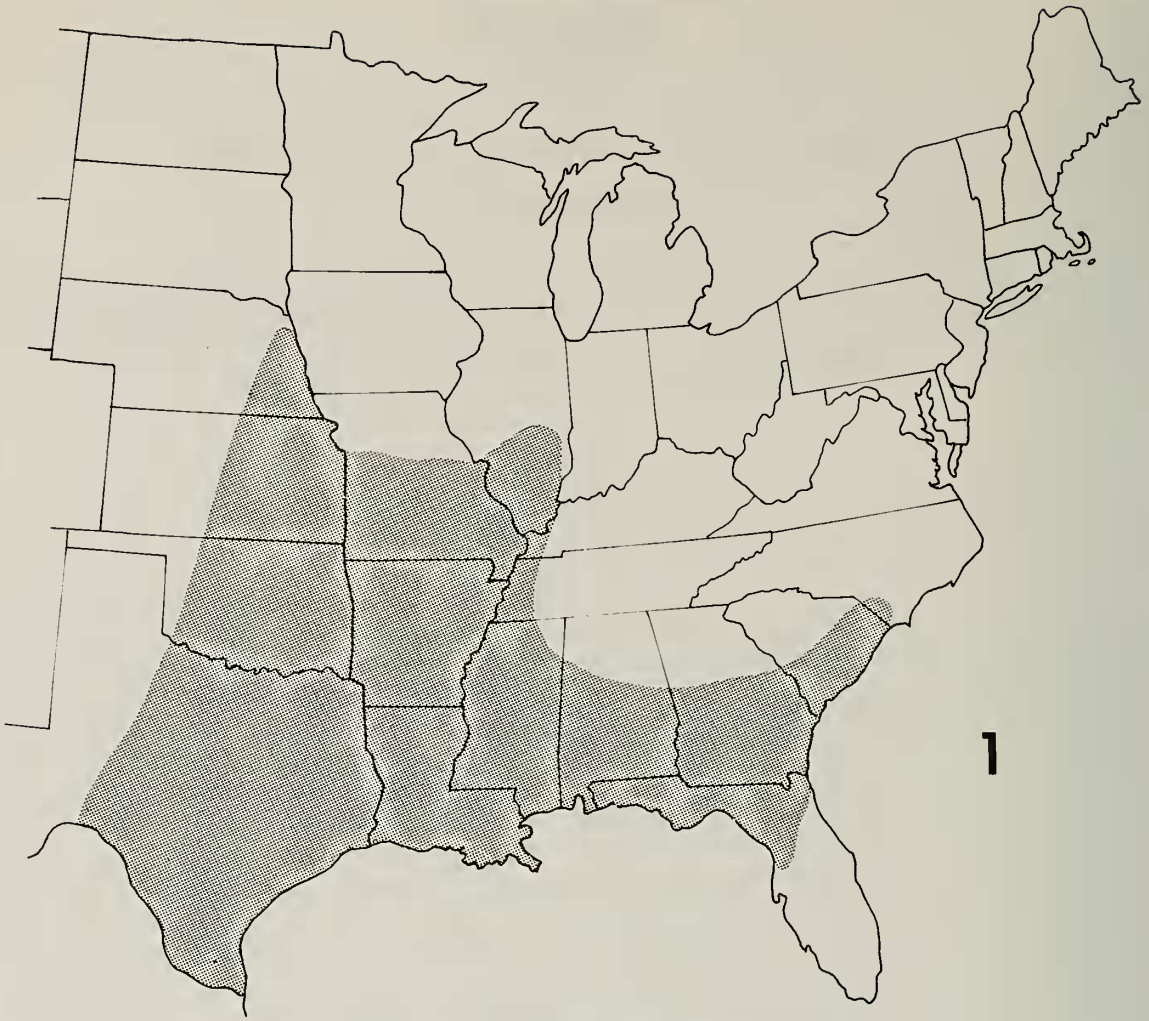


Fig. 1. Distribution of *Eurymerodesmus* and the Eurymerodesmidae.

tures, many of which are elaborately complex. *Eurymerodesmus mundus* and western populations of *E. birdi birdi*, both authored by Chamberlin (1931), exhibit enormous lobes on the caudal aperture margins that extend well below the levels of the ambulatory coxae and must therefore affect either locomotion, posture, or both (Figs. 149-151, 169-171). From spatial considerations, these species must walk "higher" for the lobes to clear the substrate. In some species lacking lobes, for example *E. oliphantus* Chamberlin, *newtonus* Chamberlin, *amplus* Causey, *varius* (McNeill), and *angularis* Causey, the sides of the apertures are divided near midlength thus forming two lateral margins along the caudal halves. The "inner lateral margin" extends variably into the opening and the "outer lateral margin" flares variably laterad thereby enclosing a cavity or "pouch" at the caudolateral

corners (Figs. 18, 21, 23, 25, 56, 59, 62, 64, 68, 73, 76-78, 84, 91). The pouches vary from open to closed depending upon the degree that the outer lateral margin leans mediad over them, and they give rise to variable tufts of hairs. Another species, *E. dactylocyphus* n. sp., lacks both of these features but possesses an exceptionally broad aperture with variably elongate flanges at the caudolateral corners; in some individuals the opening covers nearly the entire ventral breadth of the segment (Fig. 184). The anatomical wonders are not limited to males; females of *E. dactylocyphus*, *angularis*, *compressus* Causey, *impurus* (Wood), and *crassatus* n. sp. possess dactyliform projections on the cyphopod valves (Figs. 14, 27, 30, 35, 130, 187) that extend caudad in *dactylocyphus* and *compressus* well beyond the aperture margin, overlapping the succeeding two or three segments. They are so long in



some forms of *dactylocyphus* as to resemble super-numerary walking legs. When I first viewed them, I thought the specimen was a mutant. These extreme genitalic modifications in both sexes are so bizarre as to compel speculation on evolution and function, which I think relate to the recent theory of sexual selection by females propounded by Eberhardt (1985) (see sexual selection section, p. 41). Beyond these striking autapomorphies, I am equally impressed with the general hairiness of eurymerodesmids, some forms being extremely setose ventrally. The lobes in *mundus* and *b. birdi* are so densely hirsute as to obliterate the surface, and in some forms of the latter the hairs become progressively longer distad with the apical hairs being fully as long as the lobes themselves, thus effectually doubling the lengths of the structures (Fig. 155). Likewise, the tufts from the caudolateral pouches are extremely dense in some species, and in others the entire aperture margins are variably hirsute, sometimes densely so. Thus in some individuals of *oliphantus*, there are long hairs arising from the anterior and lateral rims, the outer surfaces of the sides extending well onto the metazonum, dense tufts from within the pouches, additional hairs from the inner surfaces of the outer lateral and caudal margins, and still more arising from beneath the division points on the sides (Fig. 91). In addition to these aperture hairs, there are variable and often dense tufts from sternal projections on pregonopodal and postgonopodal segments, even on relatively flat caudal segments and on females. Coupled with those on the gonopods, the overall effect of these hairs and their variations in lengths and densities is so impressive as to be a fitting source for the family-group and type genus names if the millipeds were newly discovered. *Eurymerodesmus* (-idae), literally meaning broad, unit, chain, does not begin to do justice to the anatomical marvels of these arthropods.

In addition to their unique anatomical features, eurymerodesmids are of exceptional ecological interest, because of the aforementioned diversity of their biotopes and their unusual ability to tolerate extremely arid conditions. I encountered a sizeable population of *varius varius* under a sun-baked log on dry sandy soil in Gilchrist County, Florida, and have visited areas in central and southern Texas known to harbor epigeal populations of *E. melacis* Chamberlin and Mulaik that can only be described as desert. Had I not known of the presence of *melacis*, I would have sworn that the only possible epigeal diplopods in these sandy, sagebrush en-

vironments would be desert-adapted spirostreptoids and spiroboloids. At the opposite moisture extreme, I have also collected *v. varius* from wet soil in hardwood hammocks in north Florida and *oliphantus* from a stump in a mesic deciduous woodland in southern Illinois. Likewise, I have visited areas in the Ozark and Ouachita Provinces that would be expected to contain many eurymerodesmids and diverse diplopod faunas because of the moist conditions and abundance of deciduous trees. Suffice it to say that eurymerodesmids have broad ecological tolerances, and of particular interest to North America is their abundance in the Central Plains, where they are the dominant polydesmoids.

Eurymerodesmids are among the earliest described American millipeds. The type species of the type genus, *E. hispidipes* (Wood 1864), proposed for a form from Illinois, was among the first millipeds named by an American author and one of the first species described from the New World. With over 2,000 preserved specimens, eurymerodesmids are abundantly represented in major institutional repositories in the United States, and many colleges and universities within the range have samples in insect and invertebrate collections. Despite this material and the considerable attention it has received in over 40 publications, the Eurymerodesmidae is also one of the most poorly understood of the major Nearctic milliped taxa. Thirty-two species-group names have been proposed, but only two can be confidently identified from published diagnoses. The descriptive accounts are among the worst ever published on the North American fauna, revealing little effort to identify taxonomically important structures or assess their conditions throughout the family. Likewise, the illustrations do not begin to portray diagnostic features, particularly of the apertures. Three species — *E. simplex* Chamberlin, *impurus*, and *melacis* — have not been figured, and most drawings of other species are meaningless sketches. A host of synonyms therefore exists, as few specimens or accounts were consulted before new names were validated. Finally, the general commentary is so riddled with contradictions, conflicting opinions, and outright errors that eurymerodesmid literature is not only useless but actually hinders study. It would be far easier to start with nothing than to have to determine synonymies and untangle such nomenclatorial confusion.

The taxonomic disarray results from two factors. First, like *Abacion* (Shelley 1984a) and several other Nearctic taxa, only one species was assumed to exist for many years, and this name

was routinely applied to forms throughout the generic range. Thus, *hispidipes* has been erroneously assigned to forms from Arkansas, Kansas, Louisiana, Texas, and even Illinois as recently as 1969. Since much of this material is lost, we can only infer which species actually were represented. Secondly as stated earlier, the male gonopods alone are not the principle taxonomic structures at the specific level, unlike most polydesmoid families. Specific details obtain chiefly either in the configuration of the gonopodal aperture, which extends anteriorly and compresses the prozonum into a narrow band, or in that plus aspects of the gonopods, which lack a prefemoral process. Somatically, the collum is moderately enlarged; the caudolateral corners of the paranota are broadly rounded; and the epiproct is pointed and subtriangular as in the Xystodesmidae. Eurymerodesmids vary in size from minute specimens of *v. varius* and *melacis* to such large species as *E. goodi* Causey and *dubius* Chamberlin. They tend to be smaller than most sympatric xystodesmids, but the general facies are so similar that mature specimens can easily be mistaken for juveniles of the latter. Juveniles of both families are practically indistinguishable. Despite this resemblance, the families are rarely mixed in the same sample because of their staggered life histories. Eurymerodesmids are decidedly "cold-adapted," most collections occurring between late October and early April (Fig. 210). Conversely, most xystodesmids prefer the warmer weather of late spring, summer, and early autumn. Thus, although sympatric through much of the midwestern and southeastern states, the two families tend to appear at different times of the year.

A curious feature of eurymerodesmids is their stiff, inflexible body; most I have found were tightly coiled in upper humus layers. They die and are preserved in this position, and in contrast to xystodesmids and platyrhacids, are nearly impossible to uncurl without breakage at one or more segmental junctures. Few specimens remain intact after handling or can be unrolled without breakage. Indeed, the exoskeleton will often tear or shatter before adjacent segments can be separated, and length measurements are difficult to obtain. Many workers obviously did not try to uncurl specimens, as evidenced by the unusually high percentage of sexing errors. Segment 7 is overlapped by legs from other segments, and since the gonopodal telopodites are linear and project

almost directly caudad, they are inconspicuous laterally in a tightly coiled male. Hence, these specimens are easily mistaken for females, because every segment appears to possess two pairs of legs and there are no obvious gonopods or gaps for the same. Consequently, many "female allotypes" are really male paratypes, and I know of no other helminthomorph milliped group in which so many sex notations are wrong. However, with experience and close observation, one can detect a slight gap between the legs on segment 7 and the raised aperture inside. Males also have a decidedly "flatter" appearance than females, as the paranota are broader and less depressed.

As currently understood (Hoffman 1979), the Eurymerodesmidae consists of two valid genera, *Eurymerodesmus* Brolemann (1900) and *Paresmus* Chamberlin (1942a). A third genus-group name, *Kewanius* Chamberlin (1938), was correctly synonymized with *Eurymerodesmus* by Causey (1963) and accepted by Hoffman (1979). The two valid genera are distinguished solely by the stouter telopodite of *Paresmus*, and *Eurymerodesmus* therefore contains everything that cannot be placed in the former. This distinction is unsatisfactory, since eurymerodesmid telopodites vary considerably in both length and breadth. Thus, major objectives of this revision are detailed analyses of the taxonomically important characters, and decisions on the number of component genera and the status of *Paresmus*. This genus is distinguished more by a subterminal acropodite than by breadth of the telopodite, but this condition blends into the smoothly continuous, broadly terminal acropodite of *Eurymerodesmus* through the intermediate condition represented by the type species of *Kewanius*, a narrowly terminal, discontinuous, and sharply demarcated acropodite. Hence, I regard the family as monotypic and place *Paresmus* and *Kewanius* in synonymy under *Eurymerodesmus*, which I divide into four lineages based on gonopodal features and the configurations of the apertures. These categories correspond to the subgenera or major components of *Sigmoria* (Shelley and Whitehead 1986), but I do not officially designate them as subgenera because genus-group names are only available for two. Since many new forms obviously await detection, it seems best not to validate names that may be overturned by future discoveries. Three of the lineages contain a single species group and are named for the oldest component species, which is anatomically characteristic for the assemblage; *hispidipes* constitutes a separate species group and lineage by itself,



since I cannot relate it to another congener. The fourth lineage, containing 17 species in four species groups, includes those assigned to both *Kewanius* and *Paresmus*, and hence is named the *Kewanius* lineage since there is no characteristic species and this name has priority by four years. Species groups within the *Kewanius* lineage are named for the oldest component species.

I present (Fig. 215) a diagram that I think reflects relationships among the lineages, but none of the sister branches can be unequivocally defined by autapomorphies, demonstrated by all component forms. Unique features can only be suggested for the *melacis* line. Decisions on polarities are hampered by insufficient knowledge of potential out-groups, but I think these traits are plesiomorphies rather than apomorphies. However with the possible exception of the *hispidipes* branch, the lineages are all cohesive geographic entities, partly sympatric with each other. The *birdi* and *Kewanius* lineages are incompletely detached and connect through *polkensis*, *caesariatus*, *pulaski*, and *serratus*, all showing acropodal features of the latter and aperture traits of the former. They demonstrate the phenomenon termed "incomplete synapomorphy" in *Sigmoria* (Shelley and Whitehead 1986). The *melacis* branch, however, appears completely segregated, and I consider it sister to the rest of the family.

In conducting this revision, I have attempted to apply the definitions of taxonomic categories employed by Shelley and Whitehead (1986) for *Sigmoria*. However, I have not personally collected many eurymerodesmids, and despite the substantial material, significant collecting gaps occur within the range. Consequently, I cannot determine the nature of the interfaces between many species nor the degree of incipient partitioning. Thus there are problematical areas that cannot be fully resolved in this first revision, for example between *varius* and *amplus* Causey, and among forms of *angularis*. However beyond this purely technical matter, looms the larger question of the actual status of the mostly parapatric forms, both here and within *Sigmoria*. There is no question that *birdi* and *mundus*, broadly sympatric through Kansas, Oklahoma, Texas, and Arkansas, are reproductively isolated and hence full species, but is this true for the parapatric forms in the *Kewanius* and *melacis* lineages, and should they be accorded the same status? Resolution of this question is beyond the scope of this work and requires the attention of someone more versed in theoretical concerns or in reproductive

biology of these forms. However, the "species" of the *melacis* and *Kewanius* lineages may actually be only semispecies, with the parent lineage becoming a superspecies. These categories cannot be handled nomenclaturally, so for the present I refer to all parapatric or narrowly sympatric entities that are not interconnected as species. This question bears on the composition of the genus, since I recognize 25 species. If the localized entities are only semispecies, *Eurymerodesmus* may contain as few as five species.

Like *Sigmoria*, *Eurymerodesmus* is a giant mosaic complex that blankets much of central and southeastern North America. Past workers have extracted pieces of this large puzzle that appear distinct because they possess different combinations of the features of the apertures and gonopods. Consequently, they assigned them different names, thereby adding nomenclatural confusion to an already intricate fauna. I have tried to resolve this difficult problem to the extent possible and leave a stable base for future students. However, the overriding significance of *Eurymerodesmus* and *Sigmoria* is their illumination of mosaics, a widespread phenomenon in the Diplopoda (Shelley 1989). The concluding section therefore attempts to integrate these revisions with recent treatments of other genera and suggest a different emphasis in systematic research that may stimulate interest in diplopodology.

This revision, then, provides complete descriptions or redescriptions of the family Eurymerodesmidae, the genus *Eurymerodesmus*, and all species and subspecies considered valid along with synonymies and pertinent anatomical illustrations. A key has also been formulated to facilitate determinations. A literature review and sections on anatomy and taxonomic characters, and sexual selection precede the systematic accounts, which are followed by sections on ecology, distribution, relationships, and the aforementioned conclusion. All pertinent holotypes or syntypes were examined except those of *compressus* and *Paresmus columbus* and *P. pulaski*, all authored by Causey, which are not at the published repositories and are lost. Also lost is the holotype of *P. parvicus*, whose vial actually contains a male of *Pseudopolydesmus pinetorum* (Bollman). These names were interpreted from near topotypical material, and neotypes are designated for all except *P. columbus*, assigned to synonymy under *dubius*.

In conducting this revision I was fortunate in receiving material from many large and small collections, both institutional and private. Acronyms of sources of preserved study material cited in the text are as follows:

- AMNH — American Museum of Natural History, New York, NY.
- ANSP — Academy of Natural Sciences, Philadelphia, PA.
- CAS — California Academy of Sciences, San Francisco, CA.
- EIU — Zoology Department, Eastern Illinois University, Charleston, IL.
- FMNH — Field Museum of Natural History, Chicago, IL.
- FSCA — Florida State Collection of Arthropods, Gainesville, FL.
- ILNHS — Illinois Natural History Survey, Urbana, IL.
- MCZ — Museum of Comparative Zoology, Harvard University, Cambridge, MA.
- MEM — Mississippi Entomological Museum, Mississippi State University, Starkville, MS.
- MNHP — Museum National d'Histoire Naturelle, Paris, France.
- MWSU — Zoology Department, Midwestern State University, Wichita Falls, TX.
- NCSM — North Carolina State Museum of Natural Science, Raleigh, NC.
- NMNH — National Museum of Natural History, Smithsonian Institution, Washington, DC.
- OKSU — Biology Department, Oklahoma State University, Stillwater, OK.
- RLH — Private collection of Richard L. Hoffman, Martinsville, VA.
- SFAU — Biology Department, Stephen F. Austin State University, Nacogdoches, TX.
- TAI — Biology Department, Texas A & I University, Kingsville, TX.
- TMM — Texas Memorial Museum, University of Texas, Austin, TX.
- UGA — University of Georgia Museum of Natural History, Athens, GA.
- UMO — Enns Entomological Museum, University of Missouri, Columbia, MO.
- UOK — Stovall Museum of Science and History, University of Oklahoma, Norman, OK.
- WAS — Private collection of William A. Shear, Hampden-Sydney, VA.
- WASU — James Entomological Museum, Washington State University, Pullman, WA.

#### LITERATURE REVIEW

Although eurymerodesmid millipeds have been known since 1864, when Wood described *Polydesmus hispidipes* from an unspecified site in Illinois, the family Eurymerodesmidae was established only 38 years ago (Causey 1951), nine years after Chamberlin (1942a) proposed the last genus-group name, *Paresmus*. *Eurymerodesmus* Brolemann, 1900, was designated the type-genus. In the original account, *Polydesmus hispidipes* was placed

in the nominate subgenus, but the next year Wood (1865) transferred it to the subgenus *Paradesmus* while repeating the verbal description and publishing a gonopod drawing showing the long prefemoral hairs. Wood (1867) described *Polydesmus (Polydesmus) impurus* from material collected at an unspecified locality in Texas by Dr. Gideon Lincecum, a pioneer physician and naturalist. Causey (1952a) reported that Lincecum traveled widely, that his last home was Bonham, Washington County, and that the type locality could not be determined with certainty. However, Bonham is in Fannin County, over 230 miles north of Brenham, the county seat of Washington County, and her error could be in either the town or county. By studying correspondence at the University of Texas library between Dr. Lincecum and Wood, James Reddell (pers. comm.) concluded that the type locality was Long Point, Washington County, near Brenham.

McNeil (1887) described the third eurymerodesmid, *Polydesmus varius*, from a female collected at Pensacola, Escambia County, Florida, and published two cyphopod drawings. Bollman (1888a) transferred *hispidipes* to *Leptodesmus* and noted that it is common throughout Arkansas, but as shown by material at the NMNH, this record refers to *E. pulaski* (Causey), *serratus* n. sp., and perhaps other species. Bollman (1888b) transferred *varius* to *Leptodesmus* and recorded it from Macon, Bibb County, Georgia. In 1893 he included all three previously described species and several xystodesmids as components of *Leptodesmus* and repeated the type localities of each. Two years later, Brolemann (1895) included *hispidipes* in his list of American myriapods and reported it from Louisiana, where it does not occur. As shown by his material at the MNHP, Brolemann's record refers to *E. amplus*.

In 1900, Brolemann proposed *Eurymerodesmus* as a subgenus of *Fontaria*. He illustrated the gonopod of *amplus*, which he misidentified as *hispidipes*, and noted that it did not belong in *Leptodesmus* as previously reported. Since the structure resembled a "secondary branch" of a *Fontaria* gonopod, particularly that of *E. simoni* Brolemann, a synonym of *Harpaphe haydeniana* (Wood), he provisionally included the species in *Fontaria* under the new subgenus. Brolemann listed development of the femur, absence of a "secondary ramus," and the presence of rows of long silken hairs along the "seminal canal" (= prostatic groove) nearly to the tip as diagnostic characters of the new subgenus. Thus, *hispidipes* is the type species of *Eury-*



*merodesmus* by monotypy, as noted by Jeekel (1971).

In the ensuing decade, Gunthorp (1913) reported *hispidipes* from Cowley, Douglas, and Jefferson counties, Kansas. Since his specimens are lost, I surmise from known records that the Cowley specimen was probably *mundus* and the others were probably *birdi birdi*. Brolemann (1915) elevated *Eurymerodesmus* to generic status and placed it in the tribe Rhysodesmini, subfamily Leptodesminae, family Leptodesmidae. Apparently unaware of Brolemann's work, Chamberlin (1918) recorded *L. hispidipes* from Creston, Natchitoches Parish, Louisiana, a citation based on specimens of *amplus* and *birdi*. Two years later, Chamberlin (1920) acknowledged *Eurymerodesmus* by publishing a brief diagnosis and adding the fourth species, *simplex*, from New Orleans, a locality that is probably wrong.

The period of intensive descriptive work began in 1931, when Chamberlin described *birdi* and *mundus* from Oklahoma, illustrating the gonopods and aperture lobes of each. Chamberlin (1938) established the genus *Kewanius* for *simplex* because of its "glabrous telopodite and larger basal gonopodal division." However, the telopodite, or specifically the prefemur, is really only less densely hirsute than that of *hispidipes*, not glabrous, and the "larger basal gonopodal division" probably refers to the broad clavate condition of the prefemoral stem. Causey (1963) did not think these features warranted generic distinction and placed *Kewanius* in synonymy under *Eurymerodesmus*, an action accepted by Hoffman (1979) and one that I can confirm.

In the decade of the '40's, Chamberlin and Mulaik (1941) described, but did not illustrate, *melacis* from Kerr, Boerne, Hidalgo, Kendall, Bandera, and Concho counties, Texas, without clearly specifying the type locality. Chamberlin (1942a) described and illustrated the gonopods of two new species of *Eurymerodesmus* from both Arkansas and Louisiana — *newtonus* and *oliphantus*, and *creolus* and *louisianae*, respectively — and erected *Paresmus* for a third new species from Louisiana, *parvicus*. Chamberlin (1942b) proposed *E. booneus* for unillustrated specimens from Boone County, Iowa, which are actually juvenile platyrhacids. Thus, *E. booneus* is a junior subjective synonym of *Auturus evides* (Bollman) [syn. nov.!), which is the only platyrhacid in central Iowa and is common in Boone County. Chamberlin (1943) described and illustrated *E. schmidtii* and *dubius* from Arkansas, and Loomis (1943) did likewise for *E. minimus*, from Jackson County, Florida. In 1946 Chamberlin proposed and

figured *E. christianus*, from Harrison County, Mississippi.

Descriptions of eurymerodesmids increased in the 1950's and were led by six papers by Causey, two the first year. She (1950a) described and illustrated five new Arkansas eurymerodesmids, *E. bentonus*, *spectabilis*, and *plishneri*, and *Paresmus pulaski* and *columbus*, and reported *E. hispidipes* from Dixon Springs, Pope County, Illinois, a misidentification of *oliphantus*. Later that year Causey (1950b) proposed *E. planus* for a form from Rankin County, Mississippi, and provided a lateral view of segment 7 with the gonopods projecting above the segmental margin. Causey (1951) established the family Eurymerodesmidae, listed several autapomorphies, and described and illustrated *angularis* from Arkansas. The next year Causey (1952a) published diagnoses and drawings of *E. compressus* and *wellesleybentoni*, from Arkansas, and *E. sanbernardiensis*, from Texas, along with a key to the species of *Paresmus* and notes on *P. impurus*. The last species was transferred from *Leptodesmus*, where it had been assigned by Bollman (1893). Causey (1952b) described and illustrated the fifth and final species of *Paresmus*, *polkensis*, from Polk County, Arkansas, along with *E. goodi* and *amplus* from Arkansas and Louisiana, respectively. This work also included new localities for *birdi*, *schmidtii*, *mundus*, *spectabilis*, and *dubius*, a sketch of the aperture of *oliphantus*, mislabeled as *hispidipes*, and the placement of *plishneri* in synonymy under *schmidtii*. Chamberlin (1952) reported *melacis* from Uvalde County, Texas, and reiterated the type localities for *dubius* and *schmidtii*. Causey (1954) transferred *varius* into *Eurymerodesmus* from *Leptodesmus*, recorded it from Mobile County, Alabama, and placed *minimus* in synonymy, thereby making Loomis' gonopod drawing (1943) the first of a male of *varius*. Chamberlin and Hoffman (1958) listed all eurymerodesmid species to that date with statements of type localities and distributions, and accepted the synonymies of *plishneri* with *schmidtii* and *minimus* with *varius*. The last work of the '50's recorded new localities for *melacis* in south Texas (Loomis 1959).

Interest in eurymerodesmids waned after the 1950's. Causey (1963) synonymized *Kewanius* with *Eurymerodesmus* and *spectabilis* with *christianus*, recording new localities for the latter from Louisiana, Alabama, Mississippi, and Arkansas. Next to *hispidipes*, *spectabilis* was the most widely known species at that time. Loomis (1969) described and illustrated *E. hamatilis* from Angelina County, Texas, and Stewart (1969) recorded *birdi* and

*hispidipes* from several northeastern Texas counties, the latter being misidentifications of *amplus*. Reddell (1970) reported *Eurymerodesmus* from caves in Bexar, Kerr, and Uvalde counties, Texas, all records of *melacis*. Loomis (1976) proposed the most recent new species, *E. digitatus*, from Burnet County, Texas, and appended a key to species in that state. Hoffman (1978, 1979) considered the Eurymerodesmidae a derivative of the Xystodesmidae and placed both in the superfamily Xystodesmoidea along with the Gomphodesmidae, Campodesmidae, and Oxydesmidae. In the latter work he estimated 22 species for *Eurymerodesmus*, ranging from Georgia to Arkansas and Illinois; *Paresmus* contained five species distributed from Arkansas to Texas.

Thus at this writing, the Eurymerodesmidae consists of two genera, *Eurymerodesmus* and *Paresmus*, with 23 and 5 nominal species, respectively, listed below in chronological order with synonymies, type localities, and other reported counties and states of occurrence. It is noteworthy that 12 species of *Eurymerodesmus* and three of *Paresmus* supposedly occur in Arkansas, while six and one, respectively, have been recorded from Louisiana. Causey (1940) reported *hispidipes* from Duke Forest, Durham County, in central North Carolina, a record deleted by Shelley (1978). *Eurymerodesmus varius* does occur in the southeastern corner of that state but is improbable farther inland as is *hispidipes* anywhere along the Atlantic Coast.

Genus *Eurymerodesmus* Brolemann 1900  
(= *Kewanius* Chamberlin 1938)

*E. hispidipes* (Wood 1864). Illinois without further specification. Erroneously reported from Arkansas and Louisiana in general (Bollman 1888a, Brolemann 1895), and the following states, counties, and parishes: Natchitoches Par., LA (Chamberlin 1918); Cowley, Douglas, and Jefferson cos., KS (Gunthorp 1913); Pope Co., IL (Causey 1950a); and Angelina, Nacogdoches, Rusk, Sabine, Shelby, Smith, and Upshur cos., TX (Stewart 1969).

*E. varius* (McNeill 1887) (= *E. minimus* Loomis 1943). Pensacola, Escambia Co., FL. Also recorded from Bibb Co., GA (Bollman 1888b); Jackson Co., FL (Loomis 1943); and Mobile Co., AL (Causey 1954).

*E. simplex* Chamberlin 1920. Reputedly New Orleans, Orleans Par., LA, but probably some 145 miles to the west northwest around Evangeline and Rapides parishes.

*E. birdi* Chamberlin 1931. Unspecified site in Murray Co., OK. Also reported from Seminole, Pittsburg, and Hughes cos., OK, and Sebastian, Logan, and Miller cos., AR (Causey 1952b); and Red River and Lamar cos., TX (Stewart 1969).

*E. mundus* Chamberlin 1931. University (of Oklahoma), Norman, Cleveland Co., OK. Also recorded from the Wichita National Forest, now National Wildlife Refuge, Comanche Co., OK (Chamberlin 1931); and Latimer, Caddo, and McClain cos., OK, and Sevier Co., AR (Causey 1952b).

*E. melacis* Chamberlin and Mulaik 1941. Type locality not specified in description, and two samples are labeled "holotype": a female from Raven Ranch, Kerr Co., TX, the first site listed in the account and which was recorded as the type locality by Chamberlin and Hoffman (1958), and a male from Edinburg, Hidalgo Co., TX. Also reported from Kendall, Bandera, and Concho cos., TX (Chamberlin and Mulaik 1941); Uvalde Co. (Chamberlin 1952); Comal and Guadalupe cos. (Loomis 1959); and caves in Bexar, Kerr, and Uvalde cos. (Reddell 1970).

*E. newtonus* Chamberlin 1942a. 1.2 mi. S Jasper, Newton Co., AR.

*E. oliphantus* Chamberlin 1942a. 15 mi. SW Oliphant, Jackson Co., AR.

*E. creolus* Chamberlin 1942a. 5 mi. NW Shreveport, Caddo Par., LA.

*E. louisianae* Chamberlin 1942a. 2 mi. S Saline, Natchitoches Par., LA.

*E. schmidtii* Chamberlin 1943 (= *E. plishneri* Causey 1950a). Rich Mtn., Polk Co., AR. Also recorded from Carroll and Washington cos., AR (Causey 1950a); and Franklin and Benton cos., AR (Causey 1952b).

*E. dubius* Chamberlin 1943. Delight, Pike Co., AR. Also reported from Clark, Dallas, Hot Springs, Saline, and Sevier cos., AR (Causey 1952b).

*E. christianus* Chamberlin 1946 (= *E. spectabilis* Causey 1950a). Pass Christian, Harrison Co., MS. Also cited from Columbia Co., AR (Causey 1950a); Union Co., AR, and Claiborne Par., LA (Causey 1952b); and Washington and East Baton Rouge Pars., LA, Mobile Co., AL, and Jackson Co., MS, (Causey 1963).

*E. bentonus* Causey 1950a. Monte Ne, Benton Co., AR. Also recorded from Carroll Co., AR (Causey 1950a).

*E. planus* Causey 1950b. Piney Woods, Rankin Co., MS.

*E. angularis* Causey 1951. DeValls Bluff, Prairie Co., AR.



*E. compressus* Causey 1952a. Junction City, Union Co., AR.

*E. wellesleybentoni* Causey 1952a. Helena, Phillips Co., AR.

*E. sanbernardiensis* Causey 1952a. San Bernard River at US hwy. 59, Fort Bend Co., TX.

*E. goodi* Causey 1952b. 16 mi. S Mena, Polk Co., AR.

*E. amplus* Causey 1952b. Ruston, Lincoln Par., LA.

*E. hamatilis* Loomis 1969. 8 mi. N Zavalla, Angelina Co., TX.

*E. digitatus* Loomis 1976. 5 mi. ESE Marble Falls, Burnet Co., TX.

#### Genus *Paresmus* Chamberlin 1942a.

*P. impurus* (Wood 1867). Long Point, near Brenham, Washington Co., TX.

*P. parvicus* Chamberlin 1942a. 1.5 mi. N Clay, Lincoln/Jackson Pars., LA.

*P. pulaski* Causey 1950a. 3 mi. S Sweet Home, Pulaski Co., AR. Also recorded from Sheridan Co., AR (Causey 1952b), and Grant Co., AR (Chamberlin and Hoffman 1958).

*P. columbus* Causey 1950a. 3 mi. E Magnolia, Columbia Co., AR.

*P. polkensis* Causey 1952b. 11 mi. N Mena, Polk Co., AR.

#### ANATOMY AND TAXONOMIC CHARACTERS

A family level revision is a formidable challenge, and particularly in the Eurymerodesmidae, where none of the nominal species has been characterized in accordance with modern standards and the taxonomically important characters are unknown. Nor has anyone searched for logical patterns in the different aperture types, which promise to be very useful in making determinations. Species distributions are also unknown, so geographic data cannot facilitate identifications. Finally, the higher taxa are very poorly defined. Distinctions between the genera are unclear, and although Causey (1951) listed some autapomorphies of the family, their taxonomic utilities at either the generic or specific levels have not been investigated. The more than 40 publications dealing in part with eurymerodesmids are useless for revisionary purposes, since they consist chiefly of either terse and unreliable locality references or mere validation statements for scientific names. This situation is much worse than that of the Xystodesmidae in 1974 when I began studying that

family; several genera had been revised, and the literature was reasonably advanced. Nothing definitive has been published on the Eurymerodesmidae, so my task as first reviser is to fill as many voids as possible, realizing that some will remain because of the impoverished initial level of knowledge. Thus, I first examined the available type specimens to ascertain the forms in question, since most illustrations are meaningless, uninterpretable sketches. Next came the reservoir of unstudied and unidentified material in institutional collections that, as expected, contained new forms and the answers to taxonomic questions, particularly which characters hold diagnostic utility. Because it was impossible to thoroughly investigate every potentially useful character, I review general eurymerodesmid external anatomy in this section as well as features found to be taxonomically important. Development of other potentially important characters is left to future workers.

At the outset it is informative to digress and review the historical development of taxonomic characters *per se*. Only two of the diagnostic autapomorphies were known before family status was proposed in 1951, and only one was recorded before 1943. Despite the elaborately ornamented apertures, the hairs on the prefemoral stem were the only unique feature observed by early authors. Wood (1864, 1865) noted them in the original descriptions of *hispidipes*, stating that the male genital appendages were "beset with very numerous long hairs," which are shown extending to the tip of the telopodite in his illustration (1865, fig. 48). Although the account is internally contradictory, Wood (1867) also mentioned the hairs in the description of *impurus*. McNeill (1887) did not allude to hairs in the description of *varius* because the types were females, but Brolemann (1900) used them along with the absence of a "secondary ramus," or prefemoral process, as justification for proposing *Eurymerodesmus* as a new subgenus of *Fontaria*. He provided an illustration of *amplus*, the Louisiana species that he (Brolemann 1895) recorded as *hispidipes*, and noted the presence of a row of long silken hairs along the length of the seminal branch almost to its tip. Curiously, in elevating *Eurymerodesmus* to generic status fifteen years later, Brolemann (1915) ignored the hairs, giving as his criteria a large femur supporting a short, slightly bent seminal branch without an apical opening, and adding that the secondary branch was absent. In a brief generic account and 11 subsequent species descriptions, Chamberlin (1920, 1931, 1942a, 1943)

and Chamberlin and Mulaik (1941) continued to mention the prefemoral hairs but did not cite any other autapomorphies, although Chamberlin (1931) did report and illustrate the lobes of *birdi* and *mundus*. Consequently, Loomis (1943) became the first author to note another feature when he mentioned in the description of *minimus*, a synonym of *v. varius*, that the mandibular stipes ended simply rather than in an "incurved process" as in males of *mundus* from Dallas County, Texas. This statement apparently did not register with Chamberlin (1946), as he said nothing about the mandible in the description of *christianus*. Thus, the recognition of the uniqueness of *Eurymerodesmus* must be attributed to Causey (1950a), who noted in a brief generic account that the gonopodal opening was variously modified posteriorly and laterally with setose lobes, that the telopodite was a "single, unbranched, slender blade with setae usually in rows," and that the leg femora, presumably meaning prefemora, were unspined. She did not include the mandibular projection in the generic account but characterized and/or illustrated it and the second leg coxa in all six descriptions that year (Causey 1950a, b). The following year, Causey (1951) erected the family and listed most of the autapomorphous features, which she characterized in the six species proposed the next year (Causey 1952a, b). Thus, 79 years elapsed from the date of the first species until a second family character was recognized, and seven more passed before other unique features were recorded. Only 87 years later was *Eurymerodesmus* properly assigned to a separate family. The prefemoral hairs have always been associated with *Eurymerodesmus*, but the other diagnostic characters have only been recognized in the past three to four decades. Developing these as fully as possible is a major objective of this work.

**Body size.** — Individual body size is a subjective criterion at best, and particularly in the Eurymerodesmidae because of the brittleness and rigidity of most preserved specimens. Females are generally larger and more vaulted than males, but both sexes tend to fragment or even shatter with handling. One should therefore measure the length while the animal is alive or freshly killed, a task for future workers since this study is based primarily on preserved specimens. Most eurymerodesmids that I encountered alive were tightly coiled under leaves or in upper soil layers. They die and are preserved in this posture, and hence must be uncoiled for measurement and examination of the genitalia. They usually fragment during this process beyond the state where

they can be reassembled for reasonably accurate length measurements, although large species tend to be more flexible than small ones. However, despite the difficulty in measuring lengths, some species are so obviously larger or smaller than others that size alone is a clue to identity, even in the field, although it should always be confirmed by examining the genitalia. For example, because *varius* is so much shorter, one could usually distinguish it from such sympatric species as *birdi* and *angularis* in Mississippi and southeastern Louisiana. Likewise in Texas, the components of the *melacis* lineage are generally smaller than parapatric or sympatric forms of *birdi* and *amplus*. Conversely in southern Arkansas and northern Louisiana, *angularis*, *compressus*, *goodi*, *dubius*, and *polkensis*, the largest eurymerodesmids, stand out in contrast to such smaller species as *birdi*, *mundus*, and *amplus*. Averaging all measurements of each species, I propose the following general size or length categories, to be modified by measurements of fresh material. They are useful when forms at opposing extremes, such as small or small to moderate and large, are found sympatrically.

TABLE 1. Size Categories for Species and Subspecies of *Eurymerodesmus*.

Category	Length (mm)	Species
Small	under 18.0	<i>v. varius</i> , <i>varius christianus</i> , <i>varius intergrades</i> , <i>melacis</i> , <i>clavatus</i> .
Small to Moderate	ca. 19-23	<i>hispidipes</i> , <i>varius louisianae</i> , <i>oliphantus</i> , <i>elevatus</i> , <i>dactylocyphus</i> , <i>sanbernardiensis</i> , <i>digitatus</i> .
Moderate	ca. 25-30	<i>impurus</i> , <i>amplus</i> , <i>newtonus</i> , <i>simplex</i> , <i>caesariatus</i> , <i>birdi</i> , <i>mundus</i> .
Moderately Large	ca. 30-32	<i>parvicus</i> , <i>crassatus</i> , <i>pulaski</i> , <i>seratus</i> .
Large	above 32	<i>angularis</i> , <i>compressus</i> , <i>goodi</i> , <i>dubius</i> , <i>polkensis</i> .

**Head.** — The head of eurymerodesmids, which is smooth and glossy with few facial setae, can easily be mistaken for that of a xystodesmid. The epicranial suture is distinct, bifid, and terminates in the interantennal region. The epicranial and interantennal setal series are usually absent; subantennal setae, one per side, are usually present; and when present, frontal and genal setae are few in number. The genae may or may not have faint central impressions, and the ends are rounded and extend beyond the adjacent cranial margins. As in xystodesmids, the antennae are long and slender, becoming progressively more hirsute distally, with antennomeres



2-6 being clavate. The four terminal cones are the only apparent sensory structures.

**Projection of the mandibular stipes.** — In both sexes the mandibular stipes possesses a mid-ventral ridge that becomes broader distad, extending beyond the corner of the stipes into a medially directed process. The projection is distinct and extends well beyond the stipes in most males, whereas it is a rounded indistinct vestige in nearly all females. The projection in males may have more taxonomic utility than currently realized, and future workers may devise a quantifying index for identifications. Obvious differences in length, breadth, degree of sclerotization, apical configuration, and whether it is linear or bowed are potentially useful, but I can only note them and characterize the structure for descriptions. However, the nubbinlike projection in males of *v. varius*, *varius christianus*, and *varius* intergrades, which resembles the minute projections of females, is so much shorter as to be diagnostic for these forms. Combined with size, this structure distinguishes these forms of *varius* without examining the gonopods or apertures, but unlike other eurymerodesmids, their sexes cannot be recognized by the size and shape of the process. The other subspecies, *varius louisianae*, cannot be distinguished unerringly from sympatric congeners because its process is longer, broader, and more typically male-like. Since the projection is short and subtriangular in *clavatus*, it may also distinguish this Texas species from sympatric or parapatric congeners. However, more material is needed of *clavatus*, known only from the type locality, before this can be stated with confidence.

**Terga.** — The dorsum of eurymerodesmids closely resembles those of xystodesmids, and the two families have been confused on several occasions probably because of the triangular epiprocts and generally parallel-sided segments that taper slightly caudad. The collum is considerably broader than the succeeding terga but does not always extend below them (Fig. 89). The anterior surfaces of the paranota are excavated below the anterior corners, which are broadly rounded on all segments thus distinguishing eurymerodesmids from platyrhacids, with which they are also confused as evidenced by Chamberlin's proposal (1942a) of *booneus* for juveniles of *Auturus evides*. American platyrhacids have body dimensions similar to moderate-size eurymerodesmids, but they have a broad, truncate epiproct and small but distinct teeth on the anterior paranotal corners, which are less rounded than those of eurymerodesmids. The teeth and truncate epiproct are

clearly visible on juvenile platyrhacids like the types of *booneus* and even early instars, so these two features invariably distinguish the two families. To separate eurymerodesmids and xystodesmids, one must examine the mandibles, the legs, the pregonopodal sternal projections, or the genitalia of both sexes.

**Sterna.** — The projections of the sterna in male eurymerodesmids may also possess taxonomic utility, a decision left to future workers. In contrast to xystodesmids, the sterna of male eurymerodesmids are extremely hairy, particularly those on pregonopodal segments. Eurymerodesmids lack a projection on segment 4, but segments 5-6 display a variety of elevations ranging from broad flattened areas to moderately long knob-like projections, all shorter than the adjacent coxal widths and apically hirsute. Likewise between the 9th legs,<sup>1</sup> there are a variety of apically setose elevations and knobs, which coalesce medially in some forms of *dubius* (Figs. 49-51) into a single large projection that can be longer than the adjacent coxal widths (Fig. 50). The remaining sterna become progressively flatter posteriorly with progressively sparser hair patches subtending the coxae. This is also the condition in females, which generally lack sternal projections and have at most only slight elevations on the anterior-most segments.

**Legs.** — Eurymerodesmid legs are subsimilar in size on all segments of both sexes; none are reduced or crassate. In addition to short, cylindrical, and truncate gonapophyses, the 2nd coxae of males exhibit variable distal lobes at the anterior and/or caudal margins, with the former usually being larger (Fig. 3). Otherwise the legs lack ventral spines and tubercles, and eurymerodesmids can thus be distinguished from sympatric xystodesmids by the absence of the ventrodiscal prefemoral spines characteristic of the latter. However, the prefemora of males do have large rounded lobes on the dorsal surfaces (Fig. 4), which differ in size between species and extend caudad for varying numbers of segments. In *angularis*, *compressus*, *goodi*, and *crassatus* the lobes extend nearly to the caudalmost legs, although diminishing caudal to midlength, whereas in *clavatus*, *digitatus*, *simplex*, and *varius*, they are restricted to the anterior half of the body, the pregonopodal segments on the last species. In the other

<sup>1</sup> The gonopods in polydesmoids, located at the anterior position of segment 7, represent the highly modified 8th legs. I therefore refer to the posterior legs on segment 7, the first postgonopodal pair, as the 9th legs even though they are technically the 8th ambulatory appendages in adult males.

eurymerodesmids, the prefemoral lobes terminate from segments 10-16, 10-12 on most species. Female eurymerodesmids and both sexes of xystodesmids lack these lobes. Eurymerodesmid tarsal claws are slightly hooked, with a hint of bisinuate curvature in some species, and arise from a thickened, globose basal mass.

**Male genitalia.** — Although the female cyphopods distinguish *compressus*, *dactylocyphus*, and some forms of *amplus* and *angularis*, most of the specific characters in *Eurymerodesmus* involve aspects of the male genitalia, which in this family refers collectively to both the aperture and gonopods.

1. *Aperture.* — The configuration of the aperture, elaborately ornamented in some species, is the most obvious characteristic of the Eurymerodesmidae. Features such as the caudolateral pouches of *oliphantus*, *paroicus*, *angularis*, and some forms of *amplus*, and the lobes of *mundus* and the westernmost population of *b. birdi*, are so striking as to compel attention to their taxonomic utility and function. Aside from *hispidipes*, in which the aperture is uniformly elevated, it is hard to understand how early workers could have overlooked them. Conversely, the gonopods at first glance appear so uniform as to be virtually devoid of information, but detailed study reveals that they contain subtle taxonomic characters in contrast to the obvious features of the apertures. Thus, eurymerodesmid determinations rely chiefly on a combination of gonopodal and aperture characters.

Ironically, the intricacies of the apertures hampered revision because there are no applicable precedents. To my knowledge they are unique in the Chelodesmidea, and perhaps also in the order Polydesmida, and therefore require a new format and terminology. After pondering how to verbally portray the opening, I decided to detail sequentially the anterior, anterolateral, lateral, caudolateral, and caudal margins. In addition to structural details, they also vary in the degree of hirsuteness, which in some forms is almost as striking as the marginal configurations. Consequently, the aperture descriptions in the species accounts adhere to the following format: a) an overview of the aperture describing its basic type, the general configuration of the opening itself, width and length measurements, and if different from the opening, the general shape of the entire aperture including marginal adornments; b) the sequential description of the anterior margin, sides, caudolateral corner(s), and caudal margin; and c) a characterization of the aperture hairs in the same

sequence. I recognize two basic types of apertures, with and without divided lateral margins and caudolateral pouches. The latter category is further divided into forms with or without lobes projecting above the general marginal elevations and located from the caudolateral corner and the adjoining part of the sides to near midlength of the caudal margin. The species displaying these aperture conditions are listed in table 2. Two general areas are circumscribed in forms with caudolateral pouches — that of the opening itself, and that of the opening plus the folds, flares, and marginal adornments, referred to as the "aperture apparatus." Both types of apertures possess indentations at the midline of the anterior margin, and both extend anteriorly in the metazonum, thereby compressing the prozonum into a narrow band. This is most apparent by comparing the stricture lines in ambulatory and gonopodal segments, as shown in figures 5-6 for *hispidipes*. On midbody segments, the stricture curves smoothly and bisinuate, but on the reproductive segment, it angles anteriorly laterally, disappears near the anterolateral corner, and reappears as a short, curved, basal line on the anterior indentation. Hoffman (1979) stated that the apertures in both eurymerodesmids and holistophallids protrude into the prozonum, but my examinations show that this region is compressed in the Eurymerodesmidae. I have never been able to trace the stricture completely, but it is particularly well defined in a few

TABLE 2. Aperture conditions in *Eurymerodesmus*.

Sides divided, with pouches	Sides entire, without pouches	
	With lobes	Without lobes
<i>angularis</i>	<i>polkensis</i>	<i>hispidipes</i>
<i>compressus</i>	<i>serratus</i>	<i>impurus</i>
<i>variis</i>	<i>birdi birdi</i>	<i>goodi</i>
<i>amplus</i>	<i>mundus</i>	<i>dubius</i>
<i>newtonus</i>		<i>caesariatus</i>
<i>oliphantus</i>		<i>pulaski</i>
<i>elevatus</i>		<i>birdi planus</i>
<i>simplex</i>		<i>melacis</i>
<i>paroicus</i>		<i>dactylocyphus</i>
<i>crassatus</i>		<i>sanbernardiensis</i>
		<i>digitatus</i>
		<i>clavatus</i>

males and can be followed around the anterolateral corners to almost join the line on the anterior indentation. The broadest aperture occurs in *dactylocyphus*, where it fills the segment width in ventral view (Fig. 184), and in a few individuals the aperture extends so far anteriorly that the prozonum is reduced to a narrow sliver, the minimum necessary to maintain structural integrity of the



segment. The stricture is invisible on the anterior indentation in these males, but its greater angle laterally further suggests that the prozonum is compressed rather than penetrated.

a) *Anterior margin*. — In every species except *dactylocyphus*, where it is elevated into a narrow rim that curves around the anterolateral corners, the anterior margin is flush with the metazonal surface. All species except *caesariatus* possess a midline indentation that varies in length and breadth, and may be apically rounded to acute. In *goodi*, *polkensis*, *paroicus*, *crassatus*, *pulaski*, *serratus*, and *sanbernardiensis* it is a long, distinct projection, extending well into the opening proper (Figs. 39, 114, 123, 127, 134, 142, 191); the opposite extreme occurs in some forms of *dubius*, *varius*, and *b. birdi*, where it is slight and barely detectable (Figs. 50-51, 56, 154).

b) *Anterolateral corner*. — The anterolateral corner, broadly rounded, poorly defined, and sub-similar in nearly all species, is more abstract than real, but is nevertheless a convenient reference point for the origins of the sides or lateral margins. Except for *dactylocyphus*, where it is elevated, the corner is flush with the metazonal surface in all species, at least on the anterior part of the curvature. The lateral elevations begin near the corner in many species, rising so close in some that they can truly be said to originate there. Since this corner is unadorned in eurymerodesmids, it is omitted from the species descriptions.

c) *Lateral margins*. — The sides or lateral margins are the most variable and complex parts of the aperture. There are two basic types — divided, and undivided or entire — and the elevations begin at varying distances behind the anterolateral corner in both. In undivided forms the elevation usually continues rising to the caudolateral corner, where it can terminate as in some forms of *dubius* (Fig. 46), continue around the corner onto the caudal margin as in *hispidipes* (Fig. 6), or continue caudad, tapering to the metazonum behind the corner as in *impurus* (Fig. 11). The rate of elevation varies from uniformly flattened as in *hispidipes* (Fig. 6), to gradual as in *digitatus*, *sanbernardiensis*, and *clavatus* (Figs. 191, 198, 205), to steep as in *impurus* (Fig. 11). The elevation may also be upright as in *hispidipes* or lean slightly mediad, thus narrowing the opening, as in *serratus* and some forms of *b. birdi* (Figs. 142, 149).

In the type population of *birdi planus*, the sides are essentially flush with the metazonum throughout

their lengths (Fig. 162), and they angle caudomedial forming a heart-shaped opening in conjunction with the anterior indentation. Thus in undivided species, the angle of the sides varies from the condition in *b. planus* to nearly linear as in *hispidipes* (Fig. 6), to multiangular as in *dactylocyphus* (Fig. 184). In undivided forms the configuration of the apparatus and the opening are the same, and hence the former is omitted from species descriptions. Variation obtains in the angle or direction of the sides and the rate and lean of the elevation. The elevations, particularly slight ones, are difficult to show from above in line drawings, some of which are close approximations of the actual condition.

In species with divided lateral margins, the configuration of the apparatus usually differs from that of the opening itself; consequently, both are characterized in descriptions. The divisions occur in the caudal halves of the sides, the anterior halves resembling the condition in undivided species, with a variable elevation, which may be upright or lean over the opening. At the division point, usually the highest part of the side, the margin divides into two lateral margins that continue around the caudolateral corners to form two caudal margins. In most species the division point is clearly visible in ventral view, and the "inner lateral margin" angles into the opening, curves through the "inner caudolateral corner," and blends into the "inner caudal margin." The more variable "outer lateral margin" can continue the upward slope of the anterior part of the sides as in *elevatus* (Fig. 97), descend to a lower level as in some forms of *angularis*, *varius*, and *newtonus* (Figs. 21, 56, 84), or flare or angle sublateral to varying degrees, in some species extending well beyond the level of the stigmata, as in *oliphantus* and some forms of *amplus* (Figs. 78, 91). The "outer caudolateral corner" is more distinct than its inner counterpart and connects with the "outer caudal margin." Up to division point the rim varies from essentially smooth to slightly irregular. After division point, the inner lateral margin is always smooth, but the outer lateral margin can be as variable as the undivided part of the sides.

d) *Caudolateral corners*. — The caudolateral corner, in many species imperceptible and poorly defined, is the reference point separating the sides and caudal margin; there are inner and outer corners in forms with divided sides. The inner caudolateral corner is almost always a smoothly rounded blending of the inner lateral and caudal margins. The outer corner, however, varies from sharp as in some forms of *amplus* and *oliphantus* (Figs. 77-78, 91), to blunt in

some forms of *angularis* and *amplus* (Figs. 18, 21, 76), to poorly defined as in *newtonus* (Fig. 84). It is usually elevated above the metazonal surface, merging with the latter a short distance along the outer caudal margin. The outer and inner lateral margins are separated to varying degrees, forming a "pouch" or cavity between them at the caudolateral corner. The cavity likewise varies in breadth, depth, and the degree to which it is open or closed, or obscured in ventral view, in turn reflecting the degree of lean in the outer lateral margin. For example, the pouch in *varius* is closed (Figs. 56, 64, 68), whereas that in *oliphantus* is open (Fig. 91), and the outer lateral margin angles strongly sublateral to form the broadest pouch in the genus, with the inner margin visible throughout its length. The pouch in the variant of *amplus* named *hamatilis* by Loomis (1969) (Fig. 78) is slightly less open than that of *oliphantus*. Forms with broadly open caudolateral pouches often exhibit bizarre configurations of the aperture apparatus, for example trapezoidal in some forms of *varius* and *oliphantus* (Figs. 59, 91), while the actual opening is broadly ovoid.

Thus, the caudolateral pouch is the cavity between the outer and inner margins at the caudolateral corner; it usually gives rise to variable tufts of short hairs. In most species, the two margins form the inner and outer boundaries of the cavity, and this condition is termed a "true pouch." Both *elevatus* and *impurus*, divided and undivided species, respectively, display a different pouch (Figs. 11, 97), in which the lateral elevations continue to rise caudally, and the inner surfaces are cupped and give rise to hairs. These are not true pouches because the cavity is primarily on the inner surface of the outer margin. The inner lateral margin of *elevatus* and the caudal part of the lateral margin in *impurus* form the base of the cavity rather than its inner boundary. Consequently, these pouches are anatomically different and are termed "false pouches."

The caudolateral corner in undivided species varies as in divided ones. The only other noteworthy point is that the lobe is located there in some forms of *b. birdi*.

e) *Caudal margin*. — In divided species, the caudal margins are essentially parallel and do not display striking modifications. Occasionally the outer or both margins may angle slightly caudad in the midline, even merging with the sternal projection(s) between the 9th legs as in some forms of *dubius* (Figs. 49-50). The outer caudolateral corner may be slightly elevated, but the outer caudal margin drops rapidly to the metazonal surface. The caudal

margin is more variable in undivided forms, particularly *b. birdi* and *mundus*, where extremely long lobes extend above the general marginal elevation, the locations varying from the caudolateral corner to near midline of the caudal margin. In *mundus* and the westernmost population of *b. birdi* these lobes project well below the adjacent coxal margins (Figs. 149-150, 169-170), and similar but smaller lobes occur in *polkensis*, *pulaski*, and *serratus*. The clavate lobes of *mundus* (Figs. 169-171) are always well removed from the caudolateral corner and located about 1/3 of the distance along the caudal margin. The broadly subtriangular lobes of *b. birdi* can occur from the caudolateral corner and adjacent part of the sides to well along the caudal margin. As seen in caudal profile, they can be in alignment with the succeeding sternal lobes (Fig. 151) or lateral to these (Fig. 156). Another undivided species with a striking feature at the caudolateral corner and caudal margin is *dactylocyphus*. Here the sides begin to rise near midlength, accelerate and extend well ventrad near the caudolateral corner, and expand onto the caudal margin. This structure is more of a cupped flange than a lobe, and hairs arise from the concave inner surface.

f) *Aperture hairs*. — Aperture hairs are highly variable throughout *Eurymerodesmus*. In forms like *b. planus*, *digitatus*, and *clavatus* (Figs. 162, 164, 168, 198, 205), hairs occur chiefly at the caudolateral corner and adjacent parts of the sides and caudal margin. In *goodi*, hairs arise at the anterolateral corner and continue onto the caudal margin (Fig. 39), while in *angularis*, *compressus*, *oliphantus*, *simplex*, *parvicus*, *crassatus*, *b. birdi*, *mundus*, and *melacis*, the anterior margin is covered to varying degrees (Figs. 18, 32, 91, 103, 123, 127, 149, 154, 169, 178). Hairs tend to be somewhat thicker on the sides of the anterior indentation, then they taper off and occur sporadically or regularly along the anterolateral corners and anterior parts of the sides, arising both from the rims and from the outer surfaces of the sides. Densities tend to increase at or near the caudolateral corners, with tufts in the pouches coming from either the under surfaces of the outer lateral margins or from the pouches proper. In some forms of *angularis* and *varius*, the division point extends inward into the opening before dividing into inner and outer margins, and often there will be a hair tuft under this extended division point (Figs. 23, 59). On undivided species without lobes, the hair pattern tapers off on the caudal margins with at most only a few scattered hairs, usually arranged linearly. However, the lobes of *mundus* and *b. birdi* are so



densely pilose, that the surface is obliterated. Hairs begin basally, become denser and longer distad, and are directed distad. In some populations of the latter with moderate-size lobes, the distal hairs are as long as the lobes themselves (Fig. 155).

2. *Gonopods*. — Eurymerodesmid gonopods are undivided, linear to gently curved structures without a solenomerite or prefemoral process, and feature long hairs that extend distad along the prefemoral stem. They are oriented laterally *in situ* with the cannula on the lateral rather than the medial side as in other chelodesmoids, and the telopodites project caudad from the aperture instead of anteriad as in other chelodesmoids. The condition in the Eurymerodesmidae therefore represents a 180° rotation in that both the cannula and telopodite have moved to opposite sides of the aperture; the coxa is also twisted so that the cannula is exposed *in situ* instead of being only slightly visible on the side of the coxa. In eurymerodesmids, the telopodites overhang and extend beyond the caudal aperture margin(s) (Figs. 6, 11, 21, 59, etc.), in many overlapping the 9th coxae or the intervening sternum. However, this also partly reflects compression of the body segments; occasionally, the anterior segments are so tightly coiled that the telopodites overhang segment 8. In *dactylocyphus*, *goodi*, and a few other species, especially those in the *melacis* lineage, the telopodites terminate before the caudal margin and are wholly enclosed by the aperture (Figs. 39, 184, 191, 205), a condition caused by a very broad aperture and short telopodites. The only exception to the caudal orientation is *caesariatus* (Fig. 117), in which the short telopodites extend directly ventrad, although in a two dimensional drawing they appear to be directed anteriad.

*In situ* configurations vary from parallel and narrowly to widely separated (Figs. 18, 32, 91, 123, 127), to overlapping in the midline (Figs. 21, 59, 73, 76, 149). These arrangements seem to have little taxonomic utility, but *paroicus* and *crassatus*, with the broadest, heaviest telopodites, are the most widely segregated. Telopodite apices are directed variably laterad to dorsad and are sometimes obscured by more proximal parts of the structure.

a) *Coxae*. — The coxae have no taxonomically significant features as far as I can determine. They are loosely joined by membrane with no trace of a sternal remnant and in fact are loosely held in the aperture on all sides. The membrane holding them in place tears easily, with that between the coxae being thicker and tougher. Thus to remove a single gonopod, I recommend tearing the intercoxal mem-

brane first while the structures are still attached to the inside of the aperture.

The coxae are large and globular, lack apophyses, have a single macroseta on the dorsal surface below the base of the cannula, hence invisible *in situ*, and carry a short, broad sternal apodeme. Their lateral orientation, representing a 180° rotation from the condition in the rest of the suborder, is an important autapomorphy for the family, and the coxa has also been twisted to bring the cannula to the open or ventral surface. The unpaired macroseta constitutes another difference from the Xystodesmidae, where there are two paired macrosetae per coxa. The term, macroseta, applies to the Xystodesmidae, where it is longer and stouter than the hairs on the base of the prefemur, but it is actually a misnomer in the Eurymerodesmidae because the seta is subsimilar to the larger ones on the prefemur. However, since it carries no taxonomic value, there is no reason to coin a new term.

b) *Telopodite*. — In the ensuing descriptions, I treat the prefemur and acropodite separately, saying little about the telopodite, which contains little taxonomic information. However, the telopodites do vary greatly in length, from the short ones of the *melacis* lineage to the long ones of the *birdi* lineage. The telopodites may be essentially linear, with at most only a slight curve on the acropodite or the distal extremity of the prefemur (Figs. 47, 199), or it may curve or lean to varying degrees over the coxa (Fig. 185). It may terminate short of (Figs. 47, 86, 93, 111), or at (Figs. 98, 124) the level of the distal extremities of the hairs. In most species the prefemur comprises as much as 7/8 of the length of the telopodite (Figs. 8, 47, 119, 172, 179), but in the *impurus* group, the prefemur is much shorter, constituting from 1/2 to 3/4 of the telopodite length (Figs. 12, 24, 40). In *paroicus*, *crassatus*, *pulaski*, and *serratus*, which have subterminal acropodites, the prefemur comprises the entire length of the telopodite.

c) *Prefemur*. — The prefemur arises centrally on the ventral surface of the coxa and consists of two parts — a broad basal mass, closely appressed to, and partly submerged in, the coxa, and the distal stem, which is directed caudoventrad to ventrad. The basal mass extends mediad along the coxa, bending abruptly ventrad just before the medial coxal margin, which therefore extends beyond the bend as seen in lateral profile of some species (Figs. 69, 85, 92, 98). The basal mass is invested with long matted hairs that are half as long as the prefemoral stem in many species and are so dense that they

obscure the shape of the mass itself. The latter appears as a silhouette through the hairs, its exact boundary uncertain. The basal hairs also obscure the proximal part of the prefemoral stem in lateral view, so for drawings from this perspective one must extrapolate lines from the visible, distal part of the prefemur.

The prefemur can be of subequal width throughout, with sides roughly parallel, or it can taper or expand distad. The last condition occurs in *simplex* and *clavatus* (Figs. 104-105, 206-207), in which the prefemur expands distal to midlength into broad shoulders on the outer and inner margins, respectively. *Eurymerodesmus varius* contains intermediate forms with strong distal lobes on the outer surfaces in *v. christianus* (Fig. 65), intergrade populations with small lobes at this position (Fig. 63), and forms without a trace of a swelling, represented by some populations of the nominate subspecies (Figs. 57-58). No precursor forms are known for the clavate condition on the inner surface shown by *clavatus*.

The most striking characteristic of the prefemoral stem is the long hairs along the inner surface, a continuation of those on the basal mass. They are the only autapomorphy of the family to have been observed by early authors and have long been used to distinguish *Eurymerodesmus*. The hairs are of several different lengths and breadths, a distinction that may also possess taxonomic utility. The most conspicuous hairs on the prefemoral stem are long and broad, and I like Brolemann's characterization (1900) of long, silken hairs. Some species, for example *serratus* (Fig. 145) also display shorter, denser hairs on the stem. The broadest hairs occur in the corona of *caesariatus* (Figs. 118-119), where they are packed so tightly as to appear sclerotized. The hairs extend, usually in two rows, along the inner prefemoral surface for most of its length, or to the level of the acropodite when this structure is subterminal, thereby marking the course of the prostatic groove. In all species except *varius*, the hairs are relatively continuous and regularly arranged, with only occasional small gaps. In *varius*, however, they are sparse and sporadic (Figs. 57-58, 63, 65, 69-71). All species also have a variable tuft on the outer or medial margin at the distal extremity of the prefemur, distal to the inner hairs. The density of this distomedial tuft, the number of hairs, and the length it extends proximad vary. Some species also have two or three scattered hairs proximal to this tuft on the outer surface, occasionally extending to the basal prefemoral bend.

*d) Acropodite.* — In most species of *Eurymerodesmus*, the acropodite is very short, only about 1/4 to 1/8 of the total telopodite length. However, as the prefemur becomes shorter in the *impurus* group, the acropodite becomes correspondingly longer, constituting 1/2 to 3/4 of the length of the telopodite (Figs. 12-13, 19-20, 22, 24, 33-34, 40-41). The position and basal breadth of the acropodite are also taxonomically important. It is broadly terminal in most species, its basal width being essentially the same as the distal width of the prefemur, so that the structures blend smoothly together with an indistinct juncture. Such acropodites are described as smoothly continuous with, and poorly demarcated from, the prefemur (Fig. 47). In *varius christianus*, the acropodite is broadly terminal, but is sharply demarcated from the prefemur because of the latter's distal lobe (Fig. 65). In *simplex*, *polkensis*, and *caesariatus*, the acropodite is narrowly terminal, arising solely from the inner prefemoral margin. The outer margin terminates bluntly in *polkensis* and *caesariatus* (Figs. 111-113, 115, 118-119), and expands into a shoulder in *simplex* (Figs. 104-105). *Eurymerodesmus clavatus* is the obverse in that the narrowly terminal acropodite arises from the outer prefemoral margin with the inner surface expanded into a shoulder (Figs. 206-207). Finally, there are four species in which the acropodite is subterminal and arises from the inner margin of the prefemur at varying distances from the tip — *parvicus*, *crassatus*, *pulaski*, and *serratus*. These species demonstrate the most bizarre, apomorphic gonopods in the family, because the acropodite is also usually short, and the prefemur displays modified margins with irregularities, serrations, and/or concavities. In *pulaski* and *serratus*, the acropodite arises in a cavity on the inner prefemoral surface, which expands into a hood shielding the structure. In *pulaski* the expansion is long and narrow (Figs. 135-136, 138), but in *serratus* it is short and broad, with an intricately serrated margin (Figs. 143-145). The acropodite in *pulaski* is little more than a thickened boss, but it is longer in *serratus*, and the combined effect with the expanded hood resembles the distal configurations in the xystodesmids *Sigmoria* (*Cheiropus*) *planca* (Loomis) and *S. (C.) serrata* (Shelley) (see Shelley 1984b). Consequently, the acropodite varies from broadly terminal and poorly demarcated from the prefemur, to broadly terminal and sharply demarcated, to narrowly terminal, to subterminal. These traits and its length confer more taxonomic utility on the acropodite than the prefemur, and one's initial



observations of a eurymerodesmid should be of the acropodite and aperture. Even in broadly continuous, poorly demarcated forms, the configuration of the aperture is vitally important in distinguishing between such species as *newtonus* and *amplus*, and *melacis* and *digitatus*. The principle distinction between the first pair is the uncinat acropodite of *newtonus* (Figs. 85-86). Likewise, the acropodite bends sharply laterad from the prefemur in *melacis*, whereas it curves broadly dorsad in *digitatus* (compare Figs. 178-180 and 198-200).

In all species, the prostatic groove runs along the inner surface of the prefemur onto the acropodite and opens terminally.

**Female genitalia.** — In contrast to the Xystodesmidae, female cyphopods display several taxonomically important features. Some features allow accurate assignment to species, whereas others allow placement in a species group. Beyond the cyphopods themselves, the apertures display elevations, flares, and other marginal modifications that may also have taxonomic utility, even though they are not as spectacular as those of males. I did not thoroughly examine female apertures, and investigations of this structure are left to future workers.

The cyphopods display the basic chelodesmoid form, with two variably hirsute valves, open basally and joined distad, attached to a glabrous receptacle on the closed, usually lateral, side, with a much smaller, densely hirsute operculum basally. The *in situ* position of the cyphopods varies from transverse (Fig. 114), to along the body axis (Figs. 42, 201), to oblique (Fig. 35), and may also have taxonomic importance. Eurymerodesmid cyphopods are comparatively large, and in relation to body size are proportionally much larger than those of eastern xystodesmids. Their various parts are also proportionally large, particularly the receptacle and operculum. The latter lacks taxonomic significance, but is oblong in profile, wider centrally in head-on view, and gives rise to long curved hairs from its outer surface. Although the operculum is the smallest component of the cyphopods, it is not so minute as to be practically invisible. It is always evident in front or head-on view, and except for species in which the receptacle curves partly around it, the operculum is also clearly visible in profile.

1. *Valves.* — The valves are the dominant feature of the cyphopods, the most visible structures *in situ* and larger than the other parts combined. They are highly variable, equal or unequal in size, and the open surface is variably hirsute. The joined distal margin is elevated in many species, diagnostically so

in a few. In species like *varius*, the elevation is insignificant (Fig. 61), but in others it extends into a distinct rim that protrudes through the aperture. Such a rim is displayed by *amplus*, in which it varies from linear, to angled toward the distal corner, to angled with a short terminal papilla (Fig. 82). In some species, the distal margins of the valves are prolonged into broadly rounded lobes as in *dubius*, *goodi*, and *digitatus* (Figs. 42-43, 52, 201-202). In others, the distal corner extends into long dactyliform projections of two main types. In *impurus*, *angularis*, and possibly also *crassatus*, the projections are broad, moderately sclerotized, subequal, and bowed toward each other, the tips touching or nearly so. The stiff, rigid projections resemble opposable digits (Figs. 14, 16, 27-30, 130-132). Valves exhibiting these projections usually lie transversely in the aperture, with the projections from each valve either overlapping or lying next to each other in the midline (Figs. 14, 27, 130). In *compressus*, where the valves lie obliquely in the aperture, the corners extend into unequal, closely appressed projections. That of the inner or medial valve is shorter, subtriangular, and hidden under the very long, rigid, dactyliform extension of the outer valve, which protrudes well beyond the aperture and overhangs the succeeding segment (Figs. 35-37). A similar condition occurs in some populations of *dactylocyphus*, where each valve extends into a long, flexible, dactyliform projection, widely separated from the other, which projects caudad for two more segments (Figs. 187-189). Not all populations of *dactylocyphus* show this extreme development; forms in Victoria County, Texas, possess variable projections ranging from short papillae to longer, digitiform lobes. Regardless of length, the projections of *dactylocyphus* are flexible and widely separated, as opposed to the stiff, rigid ones of *angularis* and *compressus*.

2. *Receptacle.* — Named the "neckpiece" by Causey (1952a) in descriptions of *compressus* and *sanbernardiensis*, the receptacle is located on the closed side of the valves, which is usually lateral. It is also somewhat lower than, or proximal to, the valves and thus does not extend as far ventrad. The receptacle is glabrous, and in many species the corners of its sides curve partly around the operculum, thus partly obscuring it in profile (Figs. 15, 28, 95). In *pulaski* the sides are expanded but are not curved (Fig. 140). Since in other species the sides are neither expanded nor curved, I judge their condition to have taxonomic utility and include it in the diagnoses. In the *melacis* lineage, the receptacle is typically narrow

and compressed into the valves, so as to be barely visible in profile. In *dubius* and *goodi* the receptacle is absent.

#### SEXUAL SELECTION

I have not observed any eurymerodesmids copulating and have no direct knowledge of associated behaviors. Neither are there any published statements, so this section is purely conjectural. However, several aspects of the male and female genitalia differ significantly from those in other chelodesmoids, particularly the Xystodesmidae, and I think bear on this topic. Genetic variation is expressed in most male eurymerodesmids through aspects of the aperture rather than through details of the gonopods as in xystodesmids. Except for *varius*, the gonopods within a species are relatively constant in the Eurymerodesmidae, and *amplus*, *angularis*, *birdi*, *dactylocyphus*, and *digitatus* exhibit a spectrum of aperture variants while maintaining reasonably uniform copulatory appendages. Likewise, females of *impurus*, *angularis*, *compressus*, *crassatus*, *goodi*, *dubius*, *amplus*, *dactylocyphus*, and *digitatus* possess cyphopods in which the distal margins or corners of the valves are markedly extended, protruding through the cyphopodal aperture *in situ*. Even on species like *varius*, the margins are elevated into a variable rim. Such conditions do not occur in the Xystodesmidae, whose valves are blunt to rounded but never extended. The papillate corner of the rim in some forms of *amplus* and the long dactyliform projections of *compressus* and *dactylocyphus* have the appearance of sensory structures or "feelers," particularly those of *dactylocyphus*, which are flexible. Aside from these structural features, the entire cyphopods of many preserved eurymerodesmid females were extruded through the apertures, with the valves, receptacle, and operculum, lying outside the segment, not just the valvular projections if present. I have rarely observed this condition in xystodesmids.

With these observations of preserved specimens, I turn to the concept of sexual selection by females, advanced by Eberhard (1985) to explain why the male genitalia have species-specific forms in many animals and hence are the source of most taxonomic characters. This hypothesis holds that females discriminate among males of their own species by the structure of the latter's genitalia and that males with favored morphologies produce more offspring, thus promoting rapid, divergent evolution of the male copulatory structures. In some spiders and other

organisms the male organ is first inserted into the female before being loaded with sperm; it is then withdrawn, charged with sperm, and reinserted. This process suggests courtship via the male intromittant organ and a "testing" of its configuration by the female. The above observations of eurymerodesmids suggest a different procedure, whereby the female feels or tests the configuration of the male aperture with the cyphopod valves or the valvular projections prior to mating, since individual variation in males is expressed through the aperture. Perhaps the dactyliform appendages actually are "feelers," to test the aperture configuration in advance of mating, and the various distal modifications of the valves represent the variety of female structures that have evolved to accomplish this function.

This hypothesis can be tested in two ways. First, it implies an abundance of sensory cells and neurons in the valvular projections, which can be searched for histologically or through transmission electron microscopy. Secondly, it should be possible to visually observe some sort of pre-mating testing of the male aperture by conspecific females, particularly those of *dactylocyphus* and *compressus*, which have the longest valvular projections. Such observations should be made on captive eurymerodesmids in the laboratory, where they can be watched continuously over time. Observations in the field are more of a chance proposition dependent upon encountering a mating pair at this exact moment, and the mere act of discovery would probably interrupt mating behavior. To date no one has attempted to keep eurymerodesmids alive in a laboratory and rear them, and indeed this has been attempted on very few larger millipeds. Consequently, maintaining live colonies of eurymerodesmids and studying reproductive behavior seem fruitful subjects for future research.

#### Family EURYMERODESMIDAE Causey

*Eurymerodesmidae* Causey, 1951:69; 1952b:1; 1954:67. Chamberlin, 1952:573. Chamberlin and Hoffman, 1958:78. Loomis, 1959:161. Stewart, 1969:384. Reddell, 1970:399. Hoffman, 1979:159.

*Type Genus.* — *Eurymerodesmus* Brolemann, 1900.

*Diagnosis.* — Relatively stiff, inflexible, small to moderate-size Chelodesmidea with the following characteristics: mandibular stipes with basal ridge extending into variable projection on distal corner, usually larger in males; sterna unspined, caudal margins usually straight to slightly curved, with or without variably hirsute elevated areas, lobes, or



knob-like projections adjacent to leg coxae, narrowly or widely segregated in midline, sometimes coalesced into single large structure, projections more pronounced in males, becoming progressively smaller and less hirsute caudally; legs of normal appearance and proportions for suborder, tarsal claws uncinata to slightly bisinuate, with globose basal mass, prefemora without spines and tubercles, with broadly rounded lobes on outer surfaces of pregonopodal legs and varying numbers of postgonopodal legs in males, 2nd coxae of males with variable ventrodiscal lobes on anterior and/or caudal margins; gonopodal aperture variably hirsute, configuration highly variable, often elaborately ornamented, anterior margin usually with variable midline indentation, sides elevated to varying degrees, simple or divided to midlength into inner and outer margins, these continuing into inner and outer caudal margins and forming setose pouch or cavity at caudolateral corners, caudal margin with or without variably subtriangular to clavate, densely hirsute lobes at varying distances from caudolateral corners, lobes sometimes enormous and extending well below levels of adjacent coxae; gonopods structurally simple, oriented laterally in aperture with cannula located ventrad or ventrolaterad, connected by membrane only, no sternal remnant; coxae relatively large, without apophyses, with single macroseta located dorsad to cannula; telopodite without prefemoral process, a simple structure directed caudad to caudoventrad from aperture, usually curving near midlength to distal extremity of prefemur; latter varying from 1/3 to 7/8 of telopodite length, comprising entire structure in a few species, with long, dense, matted filiform hairs basally, usually with two to three rows of such hairs along inner margin, and variable distomedial tuft; acropodite not divided, usually varying from about 1/8 to 1/2 of total telopodite length, a very short projection or boss in a few species, usually located apically and poorly demarcated from prefemur, arising from inner prefemoral margin in some forms and subterminally in others; prostatic groove arising in basal pit in prefemur, opening terminally on acropodite; cyphopod valves usually relatively large and moderately hirsute, often with modifications on distal corners ranging from slight ridge to variable dactyliform projections protruding through aperture.

*Distribution.* — The central, southcentral, and southeastern United States, ranging from northeastern Nebraska, the Missouri River in Missouri, central Illinois, the Fall Zone region of the southeast,

and southeastern North Carolina south to northern Florida and the Rio Grande, and westward to the central Great Plains of Kansas and Oklahoma and the Edwards Plateau of Texas (Fig. 1).

*Component.* — *Eurymerodesmus* Brolemann.

### Genus *Eurymerodesmus* Brolemann

*Eurymerodesmus* Brolemann, 1900:101; 1915:554. Chamberlin, 1920:97-98. Attems, 1938:185. Causey, 1950a:267; 1952a:169; 1952b:1; 1954:67; 1963:77. Chamberlin and Hoffman, 1958:78. Jeekel, 1971:262. Loomis, 1976:287. Hoffman, 1979:159.

*Kewanius* Chamberlin, 1938:208. Chamberlin and Hoffman, 1958:82. Jeekel, 1971:268.

*Paresmus* Chamberlin, 1942b:7. Causey, 1950a:271; 1952a:174; 1952b:4. Chamberlin and Hoffman, 1958:82. Jeekel, 1971:278. Hoffman, 1979:159. **NEW SYNONYMY.**

*Type species.* — Of *Eurymerodesmus*, *Polydesmus hispidipes* Wood, by monotypy; of *Kewanius*, *Eurymerodesmus simplex* Chamberlin, by original designation; of *Paresmus*, *P. paroicus* Chamberlin, by original designation.

*Diagnosis.* — With the characters of the family.

*Color in Life.* — Variable; most forms apparently with pink, orange, or red peritremata, color extending slightly onto flattened paranotal surfaces; metaterga varying from speckled black to dark olive-green with concolorous pink, orange, or red stripes along caudal margins connecting peritrematal markings, stripes varying in width, intensity of pigmentation, and partly or completely interrupted to varying degrees by base color; collum with concolorous pink, orange, or red stripes along anterior and posterior margins.

*Description.* — A genus of small to large eurymerodesmids with the following characteristics:

Body composed of head and 20 segments in both sexes; size of mature adults varying from large, robust forms of about 6.6 mm wide and 39.5 mm long to minute ones of about 1.6 mm in width and 14.0 mm in length; W/L ratio similarly varying from about 11.3-19.7%. Body essentially parallel sided in midbody region, tapering at both ends, more so caudally.

Head of normal appearance, usually smooth and polished, occasionally partly granular. Epicranial suture distinct, terminating in interantennal region, apically bifid. Interantennal isthmus of varying width. Genae not margined laterally, with or without shallow central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins, width variable. Antennae moderately slender, varying in length, becoming progressively more hirsute distally, with four short, conical sensory cones on ultimate article, no other sensory structures apparent. Facial setae reduced; epicranial absent, clypeal and labral present, with or without interantennal, subantennal, frontal, and/or genal series. Mandibular stipes with basal ridge extending into variable projection ranging from minute, rounded, nubbinlike vestige to long, heavily sclerotized structure overhanging gnathochilarium, straight or slightly bowed inward.

Terga smooth and polished, occasionally finely granular, with only trace of wrinkling. Collum considerably longer than remaining tergites, width variable, ends subequal to or extending slightly below those of following tergite. Paranota distinct but relatively narrow; varying from flattened, subparallel to substrate, and thus interrupting slope of dorsum, to variably depressed and relatively continuous with latter; anterior corners broadly rounded on all segments, anterior surfaces excavated to varying degrees, more so in anterior half of body; posterior margins angling anteriorly through about segments 5-6, becoming straight in midbody region and angling caudad on posteriormost segments; posterior corners rounded on anteriormost segments, blunt in midbody region, becoming progressively prolonged and acute caudally. Peritremata relatively narrow but thick and conspicuous, strongly set off from paranotal surface, broader caudal to midlength; ozopores located caudal to midlength, opening laterad. Epiproct moderately long and subtriangular, apically narrow and blunt.

Sides of metazonites granular or smooth and polished, with occasional shallow, curved impressions and short, acute projections on first few segments near coxae. Strictures sharp, distinct except on gonopodal segment. Stigmata small, usually rounded. Pregonopodal sterna variously modified; those of segments 2-4 normal; 5th and 6th sterna with variably elevated, flattened areas to narrower paramedian knobs, segregated to varying degrees, elevations and knobs usually higher and more pronounced on 6th sternum, all projections variably hirsute. Postgonopodal sterna with depressions or variably hirsute elevations or projections between 9th legs, segregated to varying degrees or coalesced in midline, usually shorter than widths of adjacent coxae, occasionally subequal to or longer than latter, remaining sterna usually flat, with variably short hirsute projections, or with variable hair patches subtending coxae, becoming progressively less dense caudally, occasionally gently rounded, becoming more plate-like posteriorly, with variable transverse impressions between leg coxae, caudal margin straight in midbody region. Gonapophyses short, truncate, cylindrical, located proximad on 2nd coxae. Legs subequal, of normal length and appearance, 2nd coxae with variable distal projections on anterior and/or caudal surfaces; prefemora without ventrodiscal spines, pregonopodal prefemora with variably broad, rounded lobes on outer surfaces, continuing onto postgonopodal legs in most species and terminating around midbody region or on caudal legs, 7th and 9th prefemora occasionally with accessory hooks on anterior surfaces; other podomeres of normal size and appearance on all legs; tarsal claws hooked or slightly bisinuate, with slight to distinct basal globose enlargement. Hypoproct broadly rounded, extending slightly medially; paraprocts with margins narrowly rounded.

Gonopodal aperture extremely variable, often elaborately ornamented, compressing prozonum into variably narrow, inconspicuous band, opening broadly ovoid to elliptical, entire apparatus, including additional space of marginal enlargements, extending laterad to varying distances over pleural regions, configuration varying from essentially a simple oval or rectangle to elaborately trapezoidal; anterior margin usually flush with metazonal surface, almost always with variably broad subtriangular indentation in midline; anterolateral corner rounded, usually flush with metazonum; sides highly variable, usually flush with metazonal surface at anterolateral corner, occasionally flush throughout without modifications or elevations, usually with rim elevated beginning at various distances from anterolateral corner, upright or leaning medially to varying degrees and obscuring part of opening, raised part either of continuous height throughout or rising slowly or steeply to peak at varying distances caudal to

midlength, thereafter either dropping steeply or slowly to metazonal surface, lower elevation on sides, or curving around caudolateral corner for varying distances onto caudal margin, or with densely hirsute, variably broad, and in some forms enormous triangular or clavate lobes arising caudally on sides, at caudolateral corner, or on caudal margin, or divided near midlength with caudal parts of sides and most of caudal margin consisting of two margins, inner lateral margin either extending inward into opening then curving downward, or extending downward and curving and blending into inner caudal margin, thus essentially continuing curvature of anterolateral margin, outer lateral margin angling or flaring caudolaterad to varying degrees at varying distances from division point, either leaning over and obscuring opening or flaring outward immediately, angle of flare varying from imperceptibly slight to around 45°, extending laterad, and in some cases caudad, well beyond levels of stigmata; inner and outer margins forming variable cavities or pouches at caudolateral corners, either partly or completely obscured by angle of flare and/or lean of outer lateral margin or open with strongly flared outer lateral margin; caudolateral corner variably rounded, blunt or angled, rim flush or elevated to varying degrees and with or without lobes, usually continuous with lateral margin, forms with two margins also with inner and outer caudolateral corners, former flush with metazonal surface and usually smoothly curved, visible or obscured to varying degrees by outer lateral margin, outer caudolateral corner rounded, blunt or angled, elevated to varying degrees above metazonal surface, usually continuous with outer lateral margin; caudal margin linear or curving smoothly on anterior side of 9th legs, frequently extending caudad medially and terminating between 9th legs, occasionally merging with sternal projections between latter, margin usually elevated laterally, continuous with sides, elevations tapering or dropping abruptly to metazonal surface at varying distances from caudolateral corner, increasing in some forms into variably short to enormous triangular or clavate lobes; forms with pouches and inner and outer lateral margins also with inner and outer caudal margins, former smoothly continuous with inner lateral margin, flush with metazonal surface, either completely inside and essentially parallel to outer caudal margin or merging with latter near midline, outer caudal margin usually elevated laterad, continuous with flare or outer lateral margin at caudolateral corner, tapering to metazonal surface and continuing along anterior side of 9th legs; aperture margins variably hirsute, with or without long filiform hairs arising from rim and overhanging opening, shorter and stouter hairs on outer surfaces of lateral and/or outer lateral margins, and variably dense tufts from pouches; anterior margin often with 3-6 long hairs along indentation and scattered hairs elsewhere; lateral margin with sporadic hairs from rims on anterior halves, hairs on outer surface usually restricted to caudal halves of sides; marginal lobes densely pilose with very short hairs arising from base to tip or with hairs becoming progressively denser and longer distad; caudal margin lightly hirsute or glabrous, usually with at most only a single row of sporadic hairs. Gonopods *in situ* with telopodites curving variably caudoventrad from coxa, touching, overlapping, or narrowly or widely segregated in midline, extending over caudal margin(s) to varying degrees with apices directed sublateral or subdorsad. Coxae relatively large, usually attaching under lateral margins of aperture and directed caudomedially, cannullas located ventrolaterad to ventrad, curving ventrad and inserting into pit of prostic groove in base of prefemur, without apophyses but often extending slightly ventrad behind base of prefemur, connected by membrane only, without sternal remnant. Telopodite of variable length, terminating before, at, or beyond distal extremities of



hairs. Prefemur of variable length and width, usually comprising from 1/3 to 7/8 of telopodite length, in some forms constituting all of latter, arising ventrally on coxa and extending mediad basally, closely appressed to and slightly submerged in coxa, curving or bending ventrad at or just before medial margin of latter and continuing linearly or in slightly bowed or curved configurations, with or without slight to moderate distal lobe or shoulder on outer or inner surfaces; usually with dense mass of filamentous hairs, usually with two to three rows of long, variably spaced filamentous hairs along inner and lateral surfaces of stem demarcating prostatic groove, some forms with nearly glabrous stems or with only a few scattered hairs, usually with distomedial tuft of from 4 to 15-18 hairs. Acropodite usually subtriangular to long, slender, and subacicular, arising apically or subterminally on prefemur, when apical smoothly continuous with and poorly demarcated from prefemur, or discontinuous and sharply demarcated, restricted to inside or outside of prefemur, length varying from about 1/8 to 2/3 of telopodite length, smoothly curved to sublinear, sides tapering smoothly and continuously to variably acuminate to blunt tip; acropodite occasionally very short, nubbinlike to a rudimentary boss, arising subterminally on inner surface of prefemur, shielded by distal lobe of latter and/or submerged in cavity along inner margin. Prostatic groove arising in basal pit in prefemur, running along inner surface of latter to terminal opening on acropodite.

Females usually slightly larger than conspecific males. Agreeing essentially with latter in somatic features with following exceptions: Process of mandibular stipes usually much shorter, a small nubbinlike vestige to slightly larger rounded lobe. Paranota narrower and more strongly depressed, continuing slope of dorsum, creating appearance of more highly arched or vaulted body. Sterna usually flattened and nearly glabrous, transverse grooves less pronounced and becoming even fainter caudally, without lobes, with sparse hair patches subtending coxae, hairs becoming even sparser caudally. 2nd coxa without lobes or projections. Prefemora without lobes on outer surfaces.

Cyphopodal aperture variably rectangular, ovoid, or elliptical, sides flush with metazonal surface or moderately to strongly elevated, occasionally flared. Cyphopods *in situ* either transverse, oblique, or perpendicular to body axis, valves usually anterior/posterior to each other with edges or valvular projections visible in, or protruding through opening, valves occasionally dorsoventrad to each other in transverse arrangement with edges invisible, or arranged along body axis with valves laterad/mediad to each other and edges visible in opening; corner (tip) of receptacle often visible *in situ*. Valves varying in size, subequal to unequal with either valve larger, distal surfaces variably hirsute, hairs increasing proximad, with or without variable lobes or linear, angular, papillate, or dactyliform projections usually arising from distal margins, usually directed ventrad. Receptacle generally subtriangular, located laterad, caudad, or dorsad to valves, occasionally submerged in latter to varying degrees, usually smaller than valves, glabrous, sides either curving distad and partly enclosing or obscuring operculum or not. Operculum varying in size, small to moderately large, triangular in profile, oblong in frontal view, with long, curved hairs arising from outer surface.

*Synonymy.* — Causey (1963) placed *Kewanius* in synonymy under *Eurymerodesmus* based on an examination of the holotype of *E. simplex*, the type species. However, she gave no reasons or illustrations, merely stating that she found no characters justifying a new taxon. Hoffman (1979) retained this synonymy. *Paresmus* was proposed largely because

of the stouter gonopod of *paroicus*, the type species (Chamberlin 1942b, Causey 1950a), and Chamberlin also indicated that the structure was distally notched instead of acuminate. However, the most significant feature of *paroicus* is the subterminal acropodite (Figs. 124-125), also displayed by *pulaski* (Figs. 136, 138), described in *Paresmus* by Causey (1950a). In *polkensis*, assigned to *Paresmus* in the original description (Causey 1952b), the acropodite arises terminally but only from the inner prefemoral margin. The outer prefemoral surface forms a shoulder above the acropodite (Figs. 111-113, 115). The two other species currently in *Paresmus*, *impurus* and *columbus*, have broadly terminal acropodites, moderately wide telopodites, and are readily accommodated by *Eurymerodesmus*; the latter is placed in synonymy under *dubius*, although its type is lost and this action should be corroborated by topotypes. Thus *paroicus*, *pulaski*, and *polkensis* differ primarily in the size of the apical lobe on the outer surface of the prefemur. In the former two species it is very large, overhanging and extending well beyond the level of the acropodite, which therefore arises subterminally. In the latter species, the lobe is not expanded, does not overhang the acropodite, and therefore constitutes a shoulder. Neither Chamberlin (1920) nor Causey (1963) illustrated *simplex*, but as shown in figures 104-105, it displays the configuration of *polkensis* with a longer acropodite and a broader, clavate, and more rounded shoulder. Consequently, the form represented by *paroicus* and referable to *Paresmus*, with a subterminal acropodite and an expanded distal prefemoral lobe, can be derived from that represented by *simplex* and referable to *Kewanius* through enlargement of the prefemoral shoulder such that it extends beyond the acropodite and causes the latter to arise subterminally. Therefore, *Paresmus* should at least be considered a synonym of *Kewanius*, which has four years of priority for forms with distal prefemoral lobes or shoulders. As shown in figure 65, populations of *varius christianus* in Louisiana also display an apical lobe on the outer surface of the prefemur. This feature is less distinct in intergrade forms in Mississippi (Fig. 63), and it disappears entirely in the nominate race on the Atlantic Coast (Figs. 57-58), which is clearly referable to *Eurymerodesmus*. Thus, a transformation series exists from the subterminal acropodites of *paroicus* and *pulaski*, to the terminal ones on the inner prefemoral margins of *polkensis* and *simplex*, to the lobed forms of *varius christianus* in Louisiana, to the eastern populations of *varius varius* with broadly

terminal, poorly demarcated acropodites, subequal in width to the distal extremity of the prefemur. Consequently, it follows that *Paresmus* as well as *Kewanius* must fall as synonyms of *Eurymerodesmus*.

*Distribution.* — Same as that of the family.

*Species.* — 25, arranged into four lineages. Two species are subdivided into a total of five geographic races. Future studies based on significantly more material may show that *angularis* and *amplus* should be divided into additional localized forms, recognizable at the specific level, and undoubtedly many more localized forms remain to be discovered in the *Kewanius* and *melacis* lineages. As stated in the introduction, however, these localized forms may not possess the full properties of species and may actually constitute semispecies, in contrast to *birdi* and *mundus*, which are unquestionably reproductively isolated. Resolution of this theoretical matter is beyond the scope of the present revision, where for consistency with recent studies, particularly that on *Sigmoria* (Shelley and Whitehead 1986), I recognize all apparently distinct, localized forms as well as *birdi* and *mundus* at the specific level. Depending upon how this question is resolved, *Eurymerodesmus* will either have many more or less than 25 species, the former if the localized forms are evaluated as reproductively isolated, and the latter if they are found to be less than full species. Conceivably, *Eurymerodesmus* may have as few as five species: *hispidipes*, *birdi*, and *mundus*, plus the *melacis* and *Kewanius* lineages collectively.

*Remarks.* — Although this study is based on examinations of over 2,000 preserved specimens, *Eurymerodesmus* is far from thoroughly sampled. This is particularly apparent in southern Arkansas and northern Louisiana, the area with the most diverse fauna. Fourteen species (*mundus*, *birdi*, *angularis*, *amplus*, *dubius*, *parvicus*, *pulaski*, *crassatus*, *compressus*, *polkensis*, *goodi*, *hispidipes*, *simplex*, and *varius*), 56% of the total known fauna, occur there, with *birdi* represented by both subspecies and *varius* represented by *v. christianus* and *v. louisianae* (Fig. 211). Consequently, this region should be meticulously sampled to determine actual distributions. My brief forays into southern and central Illinois, the New Orleans region of Louisiana, and Texas south of Houston and Austin were not very productive and convinced me that adequate collecting in the areas of high diversity would take years and could only be accomplished by someone based there. The forested part of east Texas, general-

ly north of Houston and east of Dallas, is another region needing attention.

Without more material and refined knowledge of distributions, particularly in these states, decisions on affinities and compositions of lineages and species groups are tentative. Anatomical patterns can be detected in both the gonopods and the aperture, but without better knowledge of their distributions, decisions on relationships are imperfect. Another difficulty is matching sexes, since some samples may contain males of one species and females of another, for example the type series of *angularis* and *crassatus*, and the neotype sample of *pulaski*, which also contained specimens of *serratus*. Careful field work is needed to check for and record subtle differences in behavior, color patterns, and microhabitat, which may indicate different species. Some questionable samples may contain forms found close together but in different microhabitats, which cannot be determined from faded, blached specimens and without detailed habitat information on vial labels; others may contain forms from relatively close, but nevertheless distinct sites. Thus, females may not be matched with conspecific males in some species accounts, and the following descriptions and species groupings are only approximations based on the incomplete available material. There is ample room for additional investigation by someone with the time to conduct meticulous field surveys, particularly along range peripheries, and record detailed habitat and color data.

#### KEY TO SPECIES OF *Eurymerodesmus* (based primarily on adult males)

Because of great variation in such species as *angularis*, *amplus*, *birdi*, and *varius*, and phenotypic similarities between variants of others, for example between *oliphantus* and forms of *amplus*, a key to species of *Eurymerodesmus* is very difficult to devise. Few comments can be made about any one species that do not also apply to another, and the total range of variation in many species is such that little can be said that will not exclude an important variant. Added to these standard difficulties with speciose milliped genera are the complexities of the aperture and the inherent difficulties in drawing the structure, verbalizing it, and combining these into meaningful couplets. Consequently, this key has limited utility and is best viewed as an introduction, perhaps more suited to eliminating taxa than to obtaining absolute determinations. Use it to reach one or two final couplets then compare the form in ques-



tion with the appropriate illustrations and descriptive accounts for final determinations. For this purpose, I have incorporated figure references throughout the key and attempted to provide more descriptive detail on variation than usual. The distinctive cyphopods of *dactylocyphus*, *impurus*, *angularis*, *compressus*, and *amplus* are also incorporated into the key, and females of these species may be easier to recognize than males. *Eurymerodesmus varius* appears twice,

to cover forms with and without prefemoral lobes, and its three subspecies are keyed in the species account. Subspecies appear herein for *birdi*. Generalized range descriptions are also provided since the aforementioned difficulties indicate the probability of more geographically based determinations for *Eurymerodesmus* than for most revised milliped taxa.

1. Acropodite very long, comprising at least half of telopodite length (Figs. 12-13, 19-20, 22, 24, 26, 40-41) . . . . . 2  
 Acropodite much shorter, comprising much less than half of telopodite (Figs. 7-8, 33-34, 47-48, 57-58, 63, 65, 69-70, 74-75, 104-105, 111-112, 124-125, 128-129, 135-136, 143-145, 152-153, 206-207) . . . . . 4
2. Sides of aperture entire, elevating slowly to peak at or near caudolateral corner (Fig. 39); corners of cyphopod valves rounded but not extending into segregated projections (Figs. 42-44); Polk and Montgomery cos., AR . . . . . *goodi* Causey  
 Sides of aperture either slightly to moderately elevated and divided caudally into inner and outer margins forming caudolateral pouches (Figs. 18, 21, 23, 25), or undivided but greatly elevated with cupulate flange extending beyond caudolateral corner and forming an apparent but false pouch between inner surface and metazonum (Fig. 11); distal corners of cyphopod valves extending into rigid segregated projections, usually bowed towards each other with apices touching or nearly so, occasionally directed oppositely (Figs. 14, 16, 27-30) . . . . . 3
3. Sides of aperture slightly to moderately elevated and divided, with caudolateral pouches (Figs. 18, 21, 23 25); projections of cyphopod valves relatively narrow, dactyliform (Figs. 27-30); central MO to northern LA and eastern MS . . . . . *angularis* Causey  
 Sides of aperture strongly elevated but not divided, without true caudolateral pouches (Fig. 11); projections of cyphopod valves relatively broad, not dactyliform (Figs. 14-16); Brazos and Washington cos., TX . . . . . *impurus* (Wood)
4. Sides of aperture divided caudally into inner and outer margins, with variably open to closed caudolateral pouches (Figs. 56, 59, 76-78, 84, 91, 97, 103, 123) . . . . . 5  
 Sides of aperture entire, without pouches (Figs. 6, 46, 109, 117, 134, 142, 149, 157, 162, 169, 178, 184, 191) . . . . . 18
5. Acropodite essentially smoothly continuous with, and poorly demarcated from prefemur; latter with at most only very slight distal swelling on outer margin (Figs. 33-34, 47-48, 57-58, 63, 74-75, 85-86) . . . . . 6  
 Acropodite not smoothly continuous with prefemur, either subterminal (Figs. 124-125, 128-129, 135-136, 143-145); terminal and discontinuous, arising from inner prefemoral margin (Figs. 104-105, 111-113, 118-119); or terminal and continuous but sharply demarcated from prefemur, latter with strong distal lobe on outer margin (Figs. 64, 71) . . . . . 11
6. Prefemur sparsely or lightly hirsute, with light distomedial tuft and at most scattered, sporadic hairs along stem, hairs arranged irregularly, with variable and sometimes sizeable intervening gaps (Figs. 57-58, 63); southern AR and western LA to FL and NC . . . . . *varius* (McNeill)  
 Prefemur moderately to densely hirsute, with variable distomedial tuft and relatively continuous hairs along stem, hairs arranged regularly or irregularly, but without sizeable gaps (Figs. 33-34, 74-75, 85-86, 92-93, 98-99) . . . . . 7
7. Acropodite moderately long, longer than 1/4 of telopodite length, broad for most of length, compressed laterally; prefemur without trace of distal swelling (Figs. 33-34); distal corners of cyphopod valves extended into rigid, unequal, and closely appressed projections, that of outer (lateral) valve very long and narrow, dactyliform, protruding well beyond aperture and overhanging succeeding segment (Figs. 35-37); Union Co., AR . . . . . *compressus* Causey  
 Acropodite short, not more than 1/4 of telopodite length, relatively narrow with sides usually tapering rapidly, not compressed; prefemur usually with slight but detectable distal swelling (Figs. 74-75, 85-86, 92-93, 98-99); corners of cyphopod valves without dactyliform projections, either not or indistinctly extended into angular ridge, with or without terminal papilla . . . . . 8
8. Acropodite distinctly uncinat, curving downward or dorsolaterad throughout length (Figs. 85-86); caudolateral pouch partly closed, covered by lean of outer lateral margin (Fig. 84); Benton, Washington, and Newton cos., AR . . . . . *newtonus* Chamberlin  
 Acropodite either straight or curving distal to midlength (Figs. 74-75, 92-93, 98-99); caudolateral pouch closed to open (Figs. 73, 76-78, 91, 97) . . . . . 9
9. Outer lateral margin rising continuously into broad, elevated lobe at caudolateral corner, not flaring laterad; inner lateral margin forming floor of pouch, cavity mostly on cupped inner surface of elevation (Fig. 97); Cole and Morgan cos., MO . . . . . *elevatus*, new species  
 Outer lateral margin variably rising but not forming elevated lobe, flaring variably laterad; inner lateral margin forming inner edge of pouch, cavity between outer and inner margins (Figs. 73, 76-78, 91) . . . . . 10
10. Caudolateral pouch broadly open, outer lateral margin flaring strongly caudolaterad, revealing, entire inner margin in ventral view, outer surface of outer lateral margin only slightly visible (Fig. 91); corners of cyphopod valves not produced (Figs. 94-95); southern IL to north-central AR . . . . . *oliphantus* Chamberlin  
 Caudolateral pouch variable, partly open to completely closed, inner margin usually partly obscured by lean of outer lateral margin, latter with considerable part of outer surface visible in ventral view (Figs. 73, 76-78); corners of cyphopod valves either imperceptibly extended or produced into angular ridge of variable length, with or without terminal papilla (Figs. 80-82); west of Mississippi River in LA to Wood and Grimes cos., TX, with allopatric population in Mason Co, TX. . . . . *amplus* Causey

11. Acropodite arising subterminally from prefemur; latter variable distad but forming terminal part of telopodite (Figs. 124-125, 128-129, 135-136, 138, 143-145) ..... 12  
 Acropodite arising terminally, either exclusively from inner prefemoral margin (Figs. 104-105, 111-113, 115, 118-119) or sharply demarcated by strong distal lobe on outer prefemoral surface (Figs. 65, 71) ..... 15
12. Terminal part of prefemur broadly expanded, margin irregularly serrate to jagged (Figs. 143-145); Pulaski Co., AR, and Alachua Co., FL ..... *serratus*, new species  
 Terminal part of prefemur variably elongate but not expanded or wide, tapering to blunt or subacuminate tip, margins smooth (Figs. 124-125, 128-129, 135-136, 138) ..... 13
13. Acropodite a thickened inconspicuous boss hidden in excavation or concavity on inner surface of prefemur, terminal part of latter either sublinear or apically uncinata (Figs. 135-136, 138); Pulaski Co., AR ..... *pulaski* (Causey)  
 Acropodite varying from a minute nubbinlike projection to a short spur extending clearly from inner surface of prefemur; latter not excavated (Figs. 124-125, 128-129) ..... 14
14. Acropodite nubbinlike, indistinct; prefemur with inner margin irregular, terminal part broadly rounded (Figs. 128-129) ..... *crassatus*, new species  
 Acropodite a short, distinct spur; prefemur with inner margin smooth, terminal part tapering to subacuminate tip (Figs. 124-125) ..... *parvicus* (Chamberlin)
15. Acropodite broadly terminal but strongly demarcated from prefemur; latter with outer margin expanding distad into rounded lobe (Figs. 65, 71), southern AR and western LA to FL and NC ..... *varius* (McNeill)  
 Acropodite narrowly terminal, arising exclusively from inner margin of prefemur (Figs. 104-105, 111-113, 115, 118-119) ..... 16
16. Prefemur distally clavate, sides expanding throughout length to distinct shoulder on outer margin (Figs. 104-105); Evangeline Par., LA ..... *simplex* Chamberlin  
 Prefemur with sides relatively parallel throughout (Figs. 111-113, 118-119) ..... 17
17. Terminal margin of prefemur with closely packed, thick hairs forming semicircular corona, lying parallel to and partly obscuring acropodite, telopodite thus appearing to terminate in calyx; aperture without anterior indentation (Figs. 117-119); Franklin Co., MS ..... *caesariatus*, new species  
 Terminal margin of prefemur without hairs, acropodite clearly visible; aperture with anterior indentation (Figs. 109-115); Polk Co., AR ..... *polkensis* (Causey)
18. Sides of aperture and/or caudolateral corner distinctly elevated above metazonal surface, with or without lobes at corner or on caudal margin (Figs. 6, 149, 154, 157, 169) ..... 19  
 Sides of aperture and caudolateral corner essentially flush with metazonal surface (Figs. 162, 165, 178, 184, 191) ..... 21
19. Aperture without distinct lobes, marginal elevation of relatively uniform height, extending around caudolateral corner onto caudal margin (Fig. 6); Coles Co., IL, and Ashley Co., AR ..... *hispidipes* (Wood)  
 Aperture with densely hirsute, variable lobes on caudal margin or at caudolateral corner (Figs. 149, 154, 157, 169) ..... 20
20. Aperture lobes clavate, very large, clearly located on caudal margin, distinctly removed from caudolateral corner (Figs. 169-171); northeastern NE to western AR and Johnson Co., TX ..... *mundus* Chamberlin  
 Aperture lobes short to long, variably triangular, never clavate, variably higher than marginal elevation, located at caudolateral corner or on caudal margin at varying distances from latter (Figs. 149-151, 154-158); eastern KS and central MO to San Patricio Co., TX, Warren Co., MS, and Jefferson Par., LA ..... *birdi birdi* Chamberlin
21. Acropodite narrowly terminal, arising from outer surface of prefemur; latter distally clavate with shoulder on inner margin (Figs. 206-207); Austin Co., TX ..... *clavata*, new species  
 Acropodite broadly terminal, smoothly continuous with, and poorly demarcated from prefemur; latter of more or less continuous width throughout, with or without slight distal swellings but without distinct shoulder, not clavate (Figs. 163-164, 179-180, 185-186, 192-193, 199-200) ..... 22
22. Telopodites relatively long, extending distinctly beyond caudal margin of aperture and overhanging 9th coxae or sternum between same (Figs. 162, 165); Rankin Co., MS, to Orleans Par., LA ..... *birdi planus* Causey  
 Telopodites relatively short, either wholly enclosed by aperture or barely overhanging caudal margin (Fig. 178, 184, 191, 198) ..... 23
23. Aperture very broad, covering essentially entire breadth of segment in ventral view and wholly encompassing telopodites, caudolateral corners elevated into variable flange (Fig. 184); distal corners of cyphopod valves extending into variable papillate to dactyliform projections, latter flexible, protruding well beyond aperture and overhanging succeeding segments (Fig. 187); Bosque to Victoria cos., TX ..... *dactylocyphus*, new species  
 Aperture much smaller, extending to or only slightly beyond levels of stigmata, not nearly covering entire breadth of segment, telopodites either enclosed within aperture or slightly overlapping caudal margin, caudolateral corners at most only slightly elevated, not forming flange (Figs. 178, 191, 198); cyphopod valves variable but without dactyliform projections (Figs. 181-182, 194-195, 202-203) ..... 24
24. Acropodite bending strongly laterad (Figs. 178-180); Taylor to Terrell and Hidalgo cos., TX ..... *melacis* Chamberlin and Mulaik  
 Acropodite curving gently or strongly dorsad (Figs. 191-193, 198-200) ..... 25
25. Caudal margin of aperture extending caudad in midline (Fig. 191); acropodite strongly curved (Figs. 192-193); Colorado to Brazoria cos., TX ..... *sanbernadiensis* Causey  
 Caudal margin of aperture linear (Fig. 198); acropodite gently curved, nearly upright (Figs. 199-200); Comanche Co., OK, to Blanco Co., TX ..... *digitatus* Loomis



### The *Hispidipes* Lineage

With raised, vertical, laminate lateral margins that curve around the caudolateral corner for about 1/3 of the length of the caudal margin, *hispidipes* differs from all congeners and merits a separate species group and lineage, which will become the nominate subgenus if these categories are shown by future studies to warrant taxonomic recognition. In other species lacking caudolateral pouches, the aperture elevations are thicker and not laminate. The slightly higher and more densely hirsute terminus of the elevation on the caudal margin faintly suggests a lobe, a possible indication of affinity to the *birdi* lineage, most forms of which possess densely hirsute lobes in this position. The *hispidipes* lineage is composed of one species group and one species.

#### *Eurymerodesmus hispidipes* (Wood)

Figs. 2-9, 211

*Polydesmus* (*Polydesmus*) *hispidipes* Wood, 1864:7-8.

*Polydesmus* (*Paradesmus*) *hispidipes* Wood, 1865:220, fig. 48.

*Leptodesmus hispidipes*: Bollman, 1893:122.

*Eurymerodesmus hispidipes*: Brolemann, 1915:554. Attems, 1938:185, fig. 203. Chamberlin and Hoffman, 1958:191 (in part).

*Type specimens*. — Two fragmented male syntypes and segments 4-7 of one female (NMNH) collected by R. Kennicott on an unknown date from an unknown site in Illinois. Wood (1864, 1865) did not mention a holotype nor are any of the fragments so designated, and it is impossible to match pieces to form a complete individual. I therefore regard this material as syntypical. There is a jar labeled "paratype" at the ANSP, also from Illinois by R. Kennicott and therefore probably from the same series, which consists of shards and debris. The number of specimens and sexes are unknown, but I noticed nothing resembling gonopods or an aperture when sifting through it in 1987. The sample is thus useless. Wood (1864, 1865) refers to 18 males in the original descriptions, an unknown number of which is probably among the debris at the ANSP. For practical purposes only the two fragmented males at the NMNH survive.

*Diagnosis*. — A small to moderate-size species; males characterized by moderate mandibular projections; sides of aperture undivided, without caudolateral pouches, with vertical, laminate elevation curving around caudolateral corner and becoming progressively higher, terminating abruptly about 1/3 of length of caudal margin; telopodite moderately long; acropodite short, about 1/8 of telopodite

length, and broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged relatively continuously along inner surface of stem; females unknown.

*Color in Life*. — Unknown.

*Male syntypes*. — Bodies highly fragmented, lengths unmeasurable, maximum width 3.3 mm.

Head capsule smooth, polished or slightly granular, width across genal apices 2.8 mm; interantennal isthmus 0.9 mm, smooth; epicranial suture narrow, linear, terminating in interantennal region, apically bifid. Antennae reaching back to caudal margin of 2nd tergite, moderately hirsute throughout, first antennomere subglobose, 2-6 clavate, 7 short and truncate; relative lengths of antennomeres  $2=6>3=4=5>1>7$ , with four apical sensory cones, no other sensory structures evident. Genae not margined laterally, with distinct central impressions, ends broadly rounded and projecting slightly beyond adjacent cranial margins. Facial setae as follows: epicranial, interantennal, frontal, and genal absent; clypeal about 4-4; labral about 9-9. Mandibular stipes with broad projection, in lateral view overhanging lingua lamella of gnathochilarium, tapering slightly distad to rounded tip on inner corner (Fig. 2).

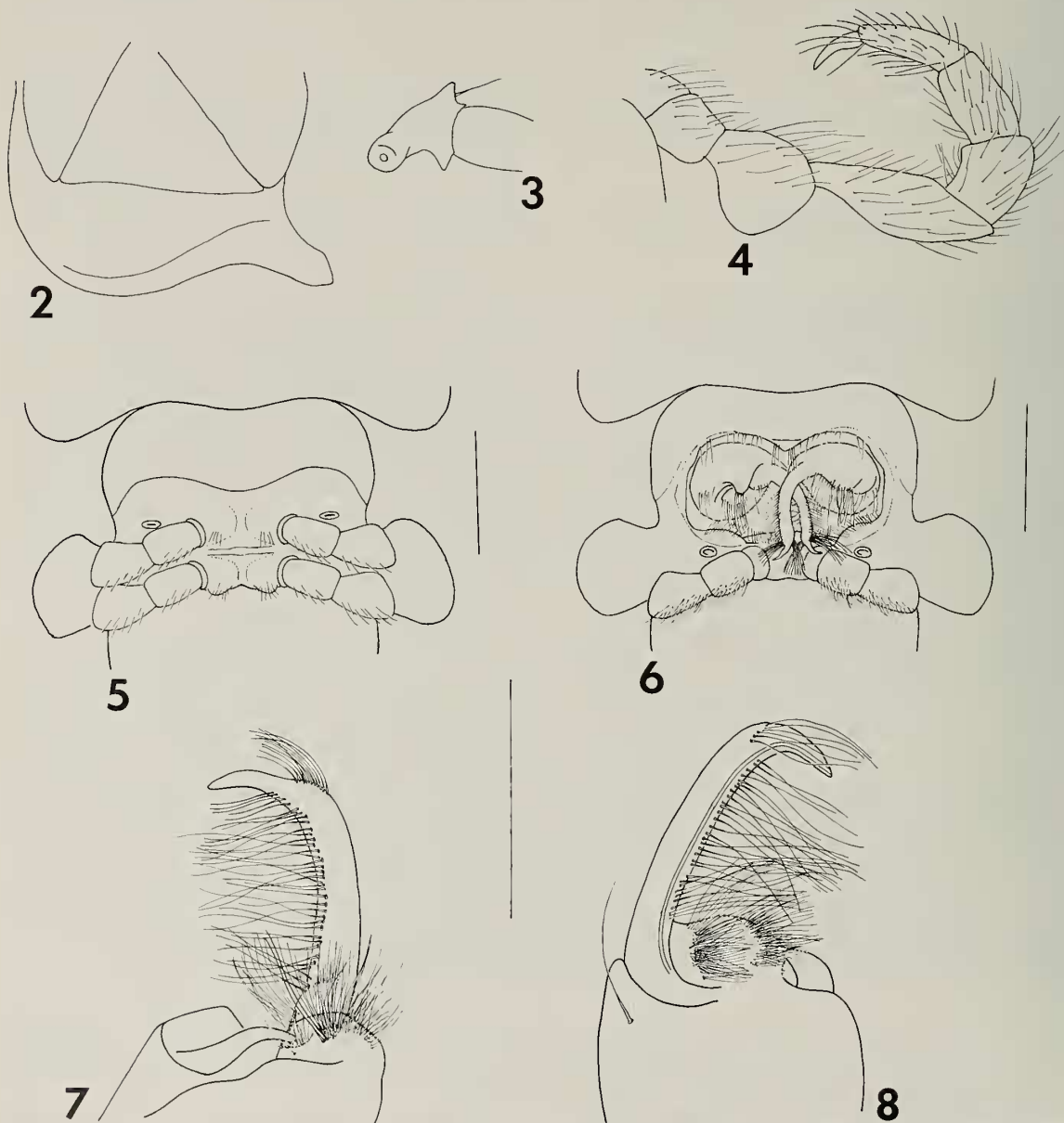
Terga smooth, polished or slightly granular; paranota with only faint wrinkling anteriorly on inner surface. Collum broad, considerably longer than succeeding tergites, ends extending slightly below those of following tergite, corners narrowly rounded. Paranota distinct but relatively narrow, flattened and subparallel to substrate, interrupting slope of dorsum; anterior corners broadly rounded with inner dorsal surface strongly excavated in anterior half of body, becoming progressively narrower, straighter, and less excavated caudally; posterior margins angling anteriorly through segment 5, corners blunt on anterior segments, becoming progressively prolonged and acute posteriorly. Peritremata relatively narrow but thick and conspicuous, strongly set off from paranotal surface, broader caudal to midlength. Ozopores located caudal to midlength, opening laterad. Epiproct moderately long and subtriangular, apically narrow and blunt.

Sides of metazonites granular, with occasional shallow, curved impressions. Strictures narrow but distinct, forming bisinuate curve on ambulatory segments (Fig. 5), displaced anteriorly by aperture on segment 7 (Fig. 6). Sternum of segment 5 slightly elevated and hirsute adjacent to leg coxae; that of segment 6 with elevations stronger, broader, and more densely hirsute. Postgonopodal sterna with transverse impressions between leg coxae varying from strong and completely crossing 8th sternum to indistinct on 18th sternum; surface otherwise flat to gently rounded, caudal margin straight in midbody region, becoming progressively more indented medially caudad. Legs without spines, moderately and relatively equally hirsute throughout, prefemora expanding into broadly rounded lobes on outer margins, lobes present on pregonopodal legs, becoming smaller in midbody region and diminishing thereafter; femur generally longer than other podomeres, tarsal claw varying from straight to moderately hooked (Fig. 4). Gonapophysis short, cylindrical, truncate; 2nd coxa with subconical distal lobes on anterior and posterior margins, former slightly larger with one seta (Fig. 3). Hypoproct broadly rounded, extending slightly mediad; paraprocts with margins slightly thickened.

Gonopodal aperture (Fig. 6) broadly ovoid, without caudolateral pouch, indented anteriorly at midline, 1.9 mm wide and 1.1 mm long at midpoint, outline of entire apparatus moderately broadly ovoid; anterior margin flush with metazonal surface, narrowing mediad and extending into opening as short,

broadly triangular projection; sides sublinear, not divided, slightly indented and flush with metazonal surface at anterolateral corners, becoming progressively more elevated caudally and continuing without interruption about 1/3 of distance onto caudal margin, essentially linear, leaning slightly over opening, rims smooth; caudolateral corner broadly rounded, nearly a right angle; caudal margin continuing elevation of sides, elevating slightly and becoming more rounded, then terminating abruptly well short of midline at about 1/3 length; margins irregularly hirsute with long hairs arising sporadically from anterior and caudal margins and overhanging opening, former with small tufts on sides of indentation and several other marginal hairs, sides relatively glabrous, caudal

margin with moderately dense tufts on elevation, hairs also arising from outer surface caudally and caudolaterally, continuing in linear arrangement along recessed part of margin between lobes. Gonopods *in situ* (Fig. 6) with telopodites directed caudoventrad, curving slightly across midline and crossing opposite member, extending over caudal margin in midline and overhanging sternum between 9th legs. Gonopod structure as follows (Figs. 7-8): Telopodite moderately long, terminating before level of distal extremities of hairs. Prefemur relatively long, about 7/8 of telopodite length, linear, tapering slightly near midlength and curving broadly caudoventrad, with two rows of long, regularly spaced hairs arising from inner margin and distomedial tuft of ten or so



Figs. 2-8. *Eurymerodesmus hispidipes*. 2, right mandibular projection of syntype, lateral view. 3, left 2nd coxa of syntype, ventral view. 4, left 7th leg of male from Coles Co., IL, caudal view. 5, segment 8 of the same, ventral view. 6, aperture and gonopods *in situ* of syntype, ventral view. 7, left gonopod of the same, lateral view. 8, the same, medial view. Scale lines for figs. 5-6 = 1.00 mm. Line for other figs. = 0.60 mm for 2-3, 0.50 mm for 4, and 1.00 mm for 7-8.



hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, arising apically at slight constriction of prefemur, directed dorsad, slightly hooked or bisinuate, tapering rapidly to subacuminate tip.

*Female Syntype.* — Among the fragments in the NMNH sample are segments 4-7 of a female, which lack structural peculiarities. The sterna resemble caudal postgonopodal sterna of males with incomplete transverse grooves between the leg pairs. Segment 3 is missing, and Wood's descriptions of the cyphopods (1864, 1865) do not reveal significant features. Thus for practical purposes, females of *hispidipes* are unknown.

*Variation.* — Wood (1864, 1865) noted differences in color among individuals in the type series. He suggested that they might represent a distinct species but did not propose a name because of similarities in the genitalia. Since all traces of color and pattern have vanished after 125 years in preservative, I cannot confirm Wood's observations. However, the gonopods of the two surviving males differ in that the acropodites of one are bisinuate and more strongly demarcated from the prefemur, while those of the other are slightly curved. The aperture configurations are practically identical. The left lateral margin of the Coles County male flares outward slightly caudolaterad, whereas the margin on the right is straight. The acropodites of this specimen are slightly bisinuate and moderately demarcated from the prefemur. The degree of hirsuteness of the aperture is subsimilar to that in the syntypes, and the only facial setae present are the clypeal (about 11-11) and labral (about 14-14) series. The Arkansas male possesses a few scattered hairs on the lateral margins, but otherwise the aperture and gonopods closely resemble those of the Coles County male. Facial setae of the Arkansas male are subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 10-10, and labral about 18-18. The specimen measures 22.0 mm in length, 3.9 mm in width, W/L ratio 17.7%.

*Ecology.* — The Coles County specimen was taken from a clod of dirt in a ploughed field. Nothing is known about the habitat of either the type series or the Arkansas specimen.

*Distribution.* — Known definitely only from Coles County, Illinois, and Ashley County, Arkansas (Fig. 9). Wood (1864, 1865) did not specify a site or general area in Illinois, and the record from Dixon Springs, Pope County (Causey 1950a, Chamberlin and Hoffman 1958), incorrectly placed in Lee County by the latter authors, refers to *oliphantus*.

Specimens were examined as follows:

ILLINOIS. Unspecified locality and date, 2M, F, R. Kennicott (NMNH) SYNTYPES and unknown number of specimens (ANSP) "PARATYPES." Coles Co., Charleston, Normal School (now Eastern Illinois University), M, 13 May 1918, T. L. H. (EIU, transferred to NCSM).

ARKANSAS. Ashley Co., 6.1 mi. E. Hamburg, M, 23 April 1965, collector unknown (FSCA).

*Remarks.* — The two known localities are separated by about 470 miles, a great distance casting doubt on the accuracy of the Arkansas record. However, other eurymerodesmids cover large areas and have samples from disparate localities known to be correct, most notably *serratus* from Pulaski County, AR, and Alachua County, FL. I therefore consider the Arkansas record to be correct and show it in the distribution map (Fig. 9).

On May 20, 1989, 81 years and one week after collection of the Coles County male, I revisited this area of eastern Illinois to attempt to secure more material, particularly of females, whose genitalia are unknown. I spent two days working in wooded areas along the Fox River and tributaries, and turning logs and rocks in clearings, all to no avail. I therefore believe that this male represents a thoroughly fortuitous discovery and that future collections are as likely to occur through chance accidents as through planned, systematic field work.

For years *hispidipes* was considered the only or most abundant species of the genus and family, and the name was routinely applied to forms in other parts of the generic range as recently as 1969, after many other nominal species had been diagnosed. I have examined the specimens on which some of these records are based and review them in Table 3 below. Others are lost but can be assigned reasonably accurately to one or two species from knowledge of distributions. All references to *hispidipes* are cited in the synonymies of the appropriate species. Since they actually refer to Wood's original citations, only Bollman (1893), Brolemann (1915), Attems (1938), and Chamberlin and Hoffman (1958) cite *hispidipes* correctly at least in part.

#### The Kewanius Lineage

I combine in one lineage all species in which the sides of the aperture are divided caudally into inner and outer margins with pouches at the caudolateral corners, or which appear related to such species through shared traits of the gonopods or aperture. The assemblage is heterogeneous, but all com-

Table 3. Previous literature citations of *hispidipes*.

Author	Date	Locality	Species
Wood	1864, 1865	Original descriptions, unspecified site in IL	<i>hispidipes</i>
Bollman	1888a	Unspecified sites in AR	<i>pulaski</i> , <i>serratus</i> , and perhaps others
Bollman	1893	Refers to original description	<i>hispidipes</i>
Brolemann	1895	Unspecified site in LA	<i>amplus</i>
Brolemann	1900	None	probably <i>amplus</i>
Gunthorp	1913	Cowley, Douglas, & Jefferson cos., KS	Cowley probably <i>mundus</i> , others probably <i>birdi</i>
Brolemann	1915	None	<i>hispidipes</i>
Chamberlin	1918	Creston, Natchitoches, Par., LA	<i>birdi</i> and <i>amplus</i>
Attems	1938	IL and LA	IL = <i>hispidipes</i> LA = <i>amplus</i>
Chamberlin	1942a	Louisiana	<i>birdi</i> and <i>amplus</i>
Causey	1950a	Dixon Springs, Pope Co., IL	<i>oliphantus</i>
Causey	1952b	aperture drawing probably of Dixon Springs male	<i>oliphantus</i>
Chamberlin & Hoffman	1958	refer to IL in general and Dixon Springs	<i>hispidipes</i> and <i>oliphantus</i>
Stewart	1969	Angelina, Nacogdoches, Rusk, Shelby, Smith, Sabine, and Upshur, cos., TX	<i>amplus</i>

ponents are linked either through the aperture, gonopods, or both, and are thus more closely related to each other than to ones in other lineages. With 17 species this is the largest branch of *Eurymerodesmus*, extending from the Atlantic seaboard to southern Illinois, central Missouri, western Arkansas, and eastern Texas. For convenience, it is divided into four species groups based on gonopod structure. It contains the second oldest species in the family, *impurus*, and the type species of the genus-group names, *Kewanius* and *Paresmus*. Since the former has priority by four years and thus is available for future subgeneric designation, it is employed here to designate the lineage.

### The *Impurus* Group

This group contains the four species of *Eurymerodesmus* with long acropodites, subequal to or only slightly shorter than the prefemora, or about 1/3 to 2/3 of the telopodite length. Since the acropodite is longer than in the other groups, the telopodite appears longer and typically extends beyond the level of the distal extremities of the hairs. The distal corners of the cyphopodal valves are moderately prolonged in *goodi* and extended into curved rigid dactyliform projections in *impurus* and *angularis*. *Eurymerodesmus compressus* has a shorter acropodite, around 3/8 of the telopodite length, but it belongs in this group because the structure is still longer than those of other groups and because its cyphopod valves are produced into long, tapered projections. That of the lateral valve is

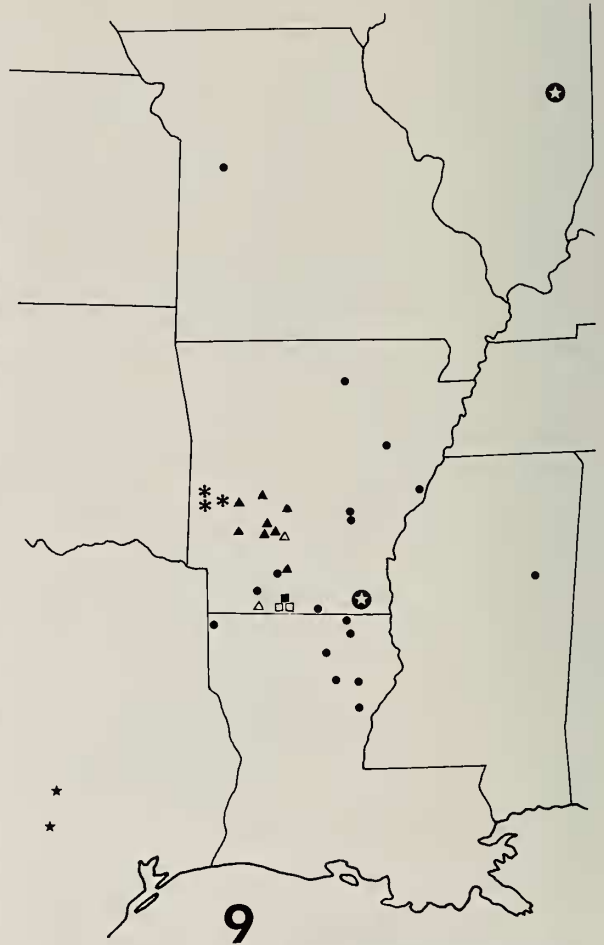


Fig. 9. Distributions of the *hispidipes* lineage, and the *impurus* and *dubius* groups. Stars in dots, *hispidipes*; stars, *impurus*; dots, *angularis*; squares, *compressus*; asterisks, *goodi*; triangles, *dubius*. Open squares and triangles denote literature records considered reliable.



longer, and that of the medial valve is closely appressed to its inner surface.

The *impurus* group occurs primarily in southern Arkansas and northern Louisiana, with outlying localities in central Missouri and north-central Mississippi. *Eurymerodesmus impurus* itself is allopatric, occurring some 240 miles to the southwest in eastern Texas adjacent to the *melacis* lineage. Additional forms with long acropodites may await discovery in northeast Texas.

*Components.* — *impurus* (Wood), *angularis* Causey, *compressus* Causey, *goodi* Causey.

***Eurymerodesmus impurus* (Wood),  
new combination  
Figs. 9-16, 212**

*Polydesmus impurus* Wood, 1867:43. Attems, 1940:493.

*Leptodesmus impurus*: Bollman, 1893:122.

*Paresmus impurus*: Causey, 1952a:174-175, figs. 8-9. Chamberlin and Hoffman, 1958:82.

*Type specimens.* — Two male syntypes (ANSP) collected by Gideon Lincecum on an unknown date in 1866 at Long Point, Washington Co., TX. The vial contains parts of two highly fragmented, incomplete males with two epiprocts, two gonopodal segments, but only one head. Both gonopods are missing from one gonopodal segment, and their location is unknown. The vial contains two labels with partly conflicting messages. One states "*Polydesmus impurus* Wood, type," and the other reads "*Leptodesmus impurus* Wood, probably type." There is a slide at the AMNH labeled "*Leptodesmus impurus* Wood, Dr. Lincecum, probably type, 1506 Phila. Acad.," which is empty but may have once contained the lost gonopods from the male at the ANSP. However, the number 1506 does not match those in the vial. The word "probably" on one label indicates some doubt that this is the type material of *impurus*, but it must be considered as such with no other specimens available.

*Diagnosis.* — A moderate-size species; males characterized by long mandibular projection; sides of aperture undivided, without true caudolateral pouches, elevating steeply and extending beyond caudolateral corner, inner surface concave thus forming false pouch; caudal margin flush with metazonal surface; telopodite long; acropodite very long, about 2/3 of telopodite length, broadly terminal, moderately demarcated from prefemur; latter with moderate number of hairs arranged continuously along inner margin; cyphopod valves of females with bowed projections from distal corners,

apices touching or nearly so; receptacle large, sides curving partly around operculum.

*Color in Life.* — Peritremata reddish; metaterga light with darker mottled areas, with reddish stripes along caudal margins connecting paranotal markings; collum with reddish stripes along both anterior and posterior margins (Wood 1867).

*Syntypes.* — Bodies highly fragmented, lengths unmeasurable, maximum width 2.8 mm.

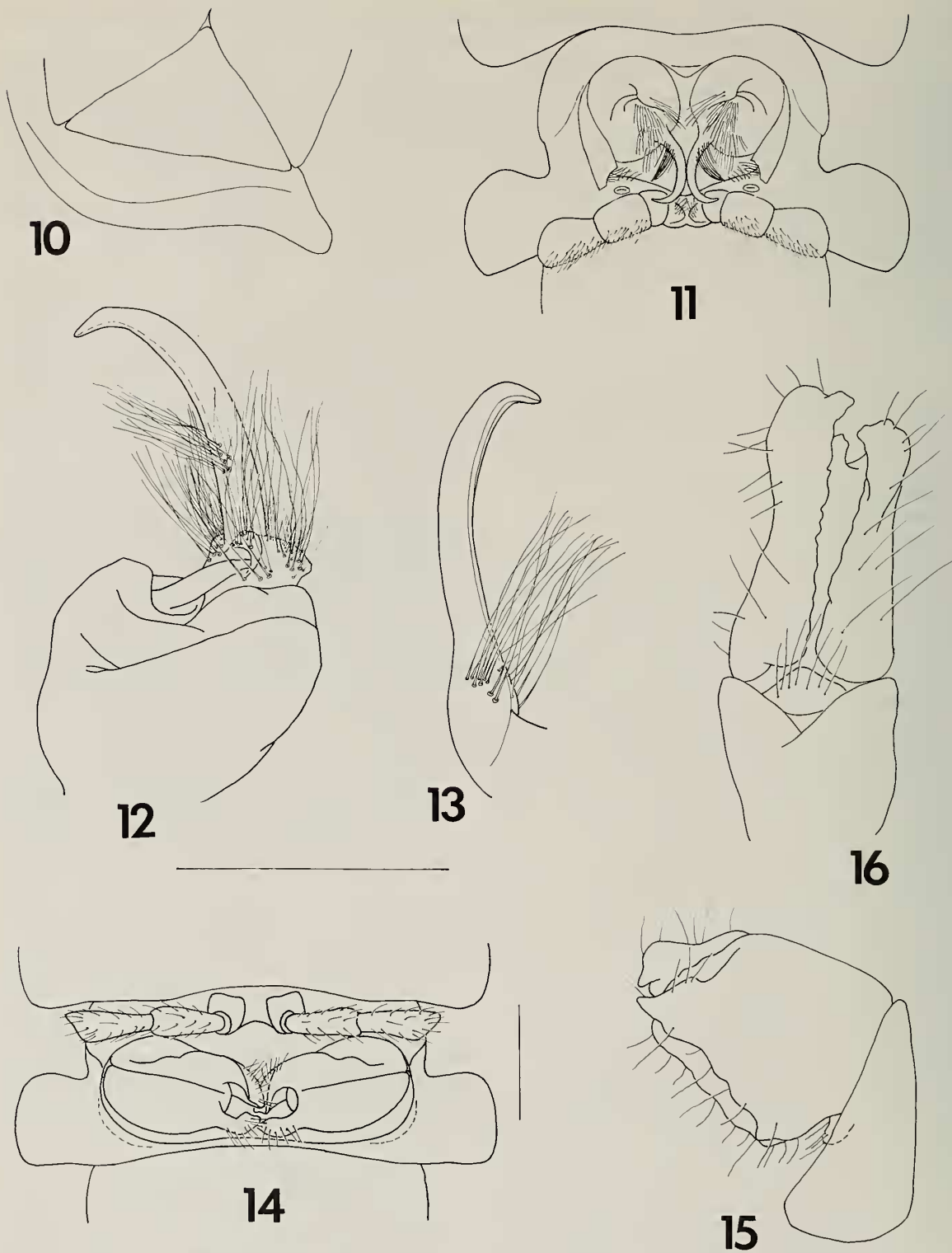
Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 1.6 mm, interantennal isthmus 0.4 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres 2>5>6>4>3>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, subantennal, frontal, and genal absent, clypeal about 8-8, labral about 14-14. Process of mandibular stipes relatively long, broadly rounded apically (Fig. 10).

Collum extending slightly below ends of following tergite. Paranota relatively flattened, interrupting slope of dorsum, posterior corners rounded to midbody segments, becoming blunt and progressively more acute thereafter.

5th and 6th sterna with low, rounded knob-like projections between both pairs of leg coxae, narrowly segregated in midline, caudal projections slightly larger than anterior ones on each segment. Postgonopodal sterna with two large, widely separated projections between 9th legs, lengths subequal to widths of adjacent coxae, with tuft of long hairs arising apically and from medial surface; remaining sterna without projections but with variable bicruciform impressions and hair patches adjacent to leg coxae, becoming flatter and more sparsely hirsute caudally. 2nd coxae with conical anterodistal projection, without caudal projection. Prefemoral lobes extending through segment 11.

Gonopodal aperture (Fig. 11) ovoid, without true caudolateral pouch but with concavity on inner surface of lateral flange, with moderate anterior indentation, 1.7 mm wide and 0.8 mm long at maxima, outline of entire apparatus rectangular; anterior indentation broadly rounded, triangular; sides not divided, elevating steeply in anterior half, leaning slightly over opening and continuing ventrad as laminate triangular flange, extending caudad beyond caudal margin, terminating abruptly, and dropping to metazonal surface beyond caudolateral corner, with shallow concavity on inner surface, rims essentially smooth; caudal margin flush with metazonal surface, discontinuous with sides, arising from inner surface of lateral flange, curving slightly caudad in midline; margins glabrous except for moderate hair tufts arising from inner surfaces of concavities of lateral flanges. Gonopods *in situ* (Fig. 11) with telopodites curving mediad, touching opposite member in midline, then curving laterad, extending beyond caudal margin of aperture and terminating over 9th coxae. Gonopod structure as follows (Figs. 12-13): Telopodite relatively long, extending just beyond level of distal extremities of hairs. Prefemur short, about 1/3 of telopodite length, terminating in slight swelling beyond ventral bend, with two rows of continuous, regularly spaced hairs along inner margin, distal tufts of 8-12 hairs on medial and lateral surfaces, and one medial hair at level of bend. Acropodite broadly terminal and very long, much longer than prefemur and about 2/3 of telopodite length, slightly narrower than distal extremity of prefemur, inner margin continuous with latter, outer margin curving inward slightly basally, leaning slightly over coxa but extending nearly directly caudad, expanding slightly



Figs. 10-16. *Eurymerodesmus impurus*. 10, right mandibular projection of male from Brazos Co., TX, lateral view. 11, aperture and gonopods *in situ* of holotype, ventral view. 12, left gonopod of the same, lateral view. 13, telopodite of the same, medial view. 14, cyphopods *in situ*, ventral view of female from Brazos Co., TX. 15, left cyphopod of the same, caudal view. 16, the same, medial view. Scale lines for figs. 11 and 14 = 1.00 mm. Line for other figs. = 0.60 mm for 10 and 15, 0.70 mm for 12 and 16, and 1.00 mm for 13.



then narrowing abruptly apically and bending sharply sublateral, tip subacuminate.

*Female from Brazos County, TX.* — Length approximately 18.7 mm, maximum width 3.2 mm, W/L ratio 17.1%. Agreeing closely with types in somatic features, with following exceptions: Genal setae 3-3. Corner of mandibular stipes slightly produced, apically blunt. Sterna flat, unmodified, glabrous.

Cyphopodal aperture elliptical, sides strongly elevated above metazonal surface. Cyphopods *in situ* (Fig. 14) with valves extruded through aperture, almost completely exposed, oriented transversely, open side directed dorsad. Valves (Figs. 15-16) large, unequal, anterior valve larger, distal corners extending into broad, curved opposing projections, that of anterior valve broader, apically blunt, and directed subcaudad, that of caudal valve more acute, curving anteriad. Receptacle large, glabrous, located lateral to valves, extending well below latter, sides curving broadly mediad and partly enveloping operculum. Latter small, tucked under open (dorsal) side of valves.

*Variation.* — Measurements of a male from Brazos County are length 27.0 mm, maximum width 4.0 mm, W/L ratio 14.8%. Facial setae include frontal and subantennal series, 1-1 each. The apertures in these males are wider than those of the types, since the lateral flanges project directly ventrad or angle sublateral instead of leaning over the opening. The apices of the flanges are squared rather than pointed, and a few scattered hairs arise from the anterior margin, the lateral rims, and the outer surfaces of the flanges. The apices of the acropodites curve more strongly than do those of the types.

*Ecology.* — According to Wood (1867), the types were collected under dried cow dung, hence the specific name. As noted by Causey (1952a), it is not unusual for millipeds to occur under dung in grassland ecosystems, where there is little other cover.

*Distribution.* — Known only from Washington and Brazos Counties, in the Coastal Plain of southeastern Texas (Figs. 9, 212). Material was examined as follows:

TEXAS: *Washington Co.*, Long Point, 2M, G. Lincecum (ANSP) TYPE LOCALITY. *Brazos Co.*, College Station, 2M, 4F, 23-24 December 1905, collector unknown (MCZ).

*Remarks.* — Wood's original description of *impurus* (1867) is internally contradictory about the gonopods. He mentions "two spines," the larger being regularly curved except apically, where it is abruptly bent. The smaller is "slender, curved, and acute." Since the telopodite is undivided, there is no prefemoral process, and the "larger" projection is clearly the telopodite, I surmise that Wood mistook one or more hairs as the second projection. Wood also contradicts himself regarding the distance that the hairs extend along the telopodite. He first states that the "blunt distal end is covered with long hairs," then mentions that neither of the "two

spines" is hairy. Only with the present illustrations can this confusion be clarified. The prefemur of *impurus* is relatively short and the acropodite comparatively long; thus the telopodite does not appear as hairy as those in other species groups.

Causey (1952a) reported that Dr. Lincecum, a pioneer physician and Texas naturalist, traveled widely in the state, that it was impossible to determine the collecting site, and that his last home was "Bonham, Washington County." However, Bonham is in Fannin County, in north Texas adjacent to Oklahoma. The town in Washington County is Brenham, and one cannot determine whether her error is in the town or county. However, the Lincecum papers at the University of Texas library reveal that, in 1866, he or a few assistants collected all the Texas myriapods described by Wood (1867) at his home in Long Point, near Brenham (J. Reddell, pers. comm.). This site is therefore the type locality.

I visited Washington County in February 1986 to try to recollect *impurus* and verify the type locality. This effort was unsuccessful, but the samples from adjacent Brazos County confirm its occurrence in Washington County. Causey (1952a) reported that the types lacked gonopods, but they were present on one specimen when I examined them in 1987, so she did not thoroughly examine the sample. Her sketches of the aperture from ventral and lateral views, some 85 years after its description, were the first illustrations of *impurus*, but they do not adequately portray the size of the lateral flange. The gonopods were omitted since she overlooked them, so the long acropodites were previously unknown, although as stated above Wood (1867) alludes confusingly to this condition in the original description. Without illustration, it is not surprising that Causey did not deduce the nature of the telopodite. The virtual absence of meaningful illustrations of the four oldest referable names — *hispidipes*, *impurus*, *varius*, and *simplex* — has greatly hampered identifications in *Eurymerodesmus* and use of these animals in other studies.

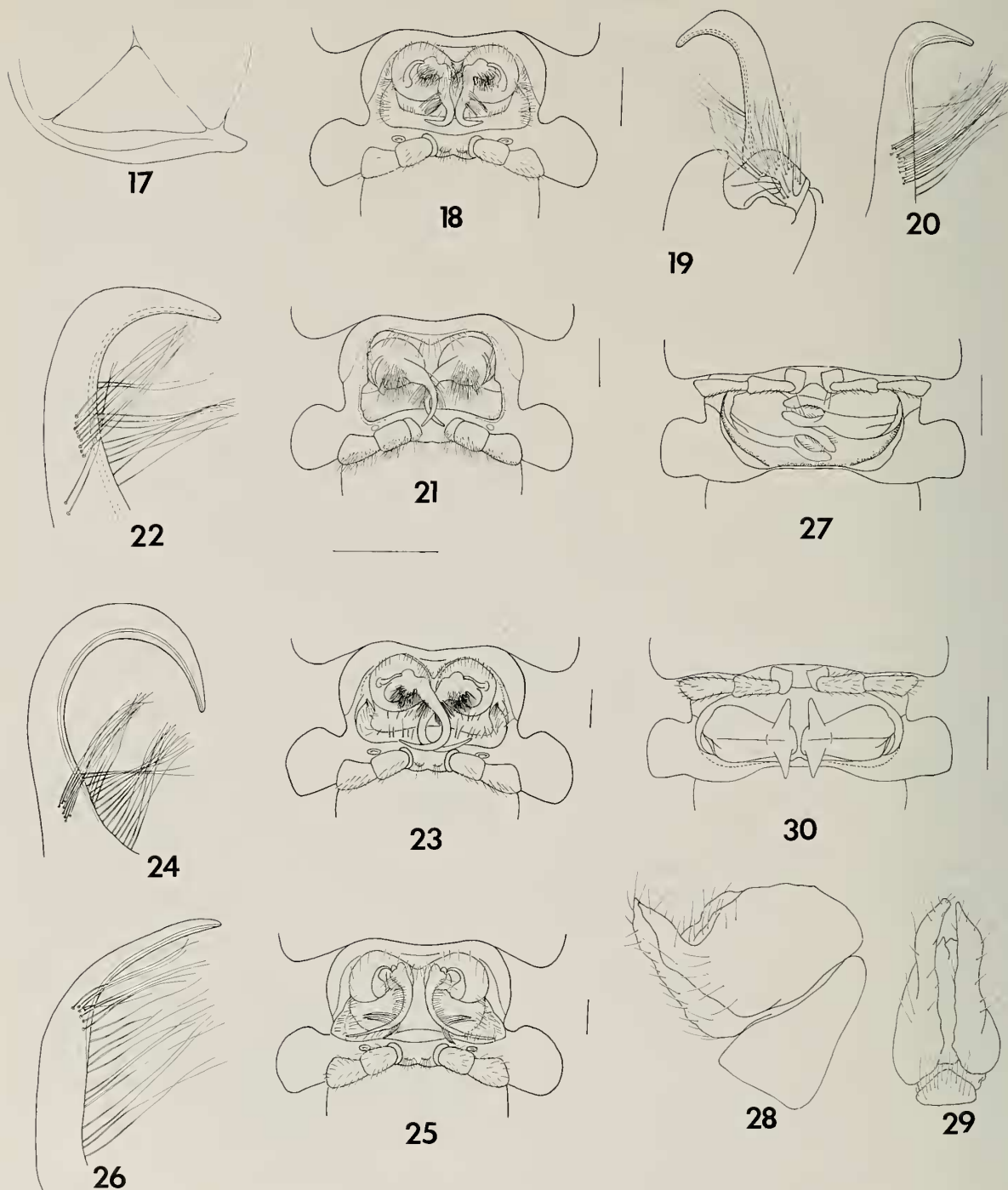
### *Eurymerodesmus angularis* Causey

Figs. 9, 17-30, 211

*Eurymerodesmus angularis* Causey, 1951:69-71, figs. 1-3. Chamberlin and Hoffman, 1958:78.

*Eurymerodesmus wellesleybentoni* Causey, 1952a:171-174, fig. 5.  
NEW SYNONYMY.

*Eurymerodesmus wellesleybentonus*: Chamberlin and Hoffman, 1958:81.



Figs. 17-30. *Eurymerodesmus angularis*. 17, right mandibular projection of male from Jefferson Co., AR, lateral view. 18, aperture and gonopods *in situ* of the same, ventral view. 19, left gonopod of the same, lateral view. 20, telopodite of the same, medial view. 21, aperture and gonopods *in situ* of male from Phillips Co., AR, ventral view. 22, telopodite of left gonopod of the same, medial view. 23, aperture and gonopods *in situ* of male from Union Co., AR, ventral view. 24, telopodite of left gonopod of the same, medial view. 25, aperture and gonopods *in situ* of male from Caddo Par., LA, ventral view. 26, telopodite of left gonopod of the same, medial view. 27, cyphopods *in situ*, ventral view of female from Jefferson Co., AR. 28, left cyphopod of the same, caudal view. 29, the same dorsomedial view. 30, cyphopods *in situ*, ventral view of female from Ouachita Par., LA. Scale lines for figs. 18, 21, 23, 25, 27, and 30 = 1.00 mm. Line for other figs. = 0.30 mm for 17 and 28-29, and 0.50 mm for 19-20, 22, 24, and 26.



*Type specimens.* — Male holotype and female allotype (ANSP) collected by L. Gray, 1 April 1950, at DeValls Bluff, Prairie Co., AR. The allotype lacks the valvular projections found on females with other males of *angularis* and probably is not conspecific with the holotype. Consequently, a specimen from adjacent Jefferson County is used for the female description.

*Diagnosis.* — A large species; males characterized by short mandibular projection; sides of aperture divided, with variably open to closed caudolateral pouches; telopodite long; acropodite variably long, 1/3 to 3/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, curving gently to strongly dorsolaterad, configuration varying from obtuse angle to falcate; prefemur with moderate number of hairs arranged continuously along inner margin; cyphopod valves of females with dactyliform projections from distal corners, varying from bowed with apices touching or nearly so to linear and directed oppositely; receptacle large, sides curving partly around operculum.

*Color in Life.* — Paranota orange; metaterga dark mottled olive to black-brown, with or without orange stripes along caudal margins; collum with orange stripe along anterior margin (Causey 1951, 1952a).

*Holotype.* — Length 36.4 mm, maximum width 4.9 mm, W/L ratio 13.5%.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 3.0 mm, interantennal isthmus 1.0 mm. Antennae reaching back to midlength of 3rd tergite, relative lengths of antennomeres 2 > 3 > 4 > 5 = 6 > 1 > 7. Genae with faint impressions. Facial setae as follows: epicranial 2-2, interantennal and genal absent, subantennal 1-1, frontal 1-1, clypeal about 11-11, labral about 23-23. Process of mandibular stipes short, broadly rounded (Fig. 17).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-11, becoming progressively more acute caudad.

5th sternum with low, sparsely hirsute, paramedian knobs between 4th legs and larger, more conical ones between 5th legs; 6th sternum with low, rounded, subequal knobs between 6th and 7th legs, each sparsely hirsute. Postgonopodal sterna with low, slightly hirsute lobes between 9th legs; segments 8-10 with minute, sparsely hirsute, paramedian knobs between anterior legs and larger, conical, sparsely hirsute knobs between caudal legs; remaining sterna with knobs between caudal legs becoming progressively shorter caudad, disappearing on segment 18. 2nd coxae with distinct, subconical anterodistal lobes and shorter, acute caudal ones. Prefemora with broad lobes on outer surfaces of all legs, becoming considerably smaller on caudalmost segments.

Gonopodal aperture (Fig. 18, not this specimen) broadly subovoid, with broad, open, caudolateral pouch and strong anterior indentation, 2.6 mm wide and 1.3 mm long at maxima, outline of

apparatus subtrapezoidal, extending laterad well beyond stigmata and cephalad nearly to anterior segmental margin, severely constricting prozonum; anterior indentation broadly triangular; sides divided, angling slightly caudolaterad and becoming increasingly elevated to division point, inner lateral margin angling dorsad into opening then curving into inner caudal margin, outer lateral margin tapering gradually dorsad, flaring strongly laterad and curving broadly into blunt caudolateral corner, forming broad, deep, open pouch with inner lateral margin, rims smooth; inner caudolateral corner blunt; outer caudolateral corner blunt; inner caudal margin sublinear, subparallel to outer caudal margin; latter sloping to metazonum, curving gently along anterior surfaces to coxal condyles, extending slightly caudad between legs; margins irregularly hirsute with long hairs arising sporadically from anterior and lateral rims and outer surfaces and overhanging opening, also with moderate tufts of hairs in caudolateral pouches and scattered hairs along outer caudal margin. Gonopods *in situ* (Fig. 18, not this specimen) with telopodites extending caudoventrad from medial margins of coxae and touching in midline, apices curving dorsolaterad over caudal margins of aperture. Gonopod structure as follows (Figs. 19-20): Telopodite moderately long, terminating at level of distal extremities of hairs. Prefemur short, approximately 1/3 of telopodite length, tapering slightly distad into indistinct medial shoulder, with two rows of continuous, regularly arranged hairs along inner margin and dense distomedial tuft of around a dozen hairs. Acropodite long and broadly terminal, about 2/3 of telopodite length, continuous with, and poorly demarcated from, prefemur, curving dorsolaterad in about a right angle proximal to midlength, narrowing continuously to subacuminate tip.

*Female from Jefferson Co.* — Length 29.9 mm, maximum width 4.1 mm, W/L ratio 13.7%. Agreeing closely with holotype in somatic features, with following exceptions: Mandibular stipes with short, acuminate process. Sterna flat, unmodified, with hair tufts adjacent to leg coxae, becoming progressively sparser caudally.

Cyphopodal aperture ovoid, sides strongly elevated above metazonal surface, thickened. Cyphopods *in situ* (Fig. 27) with valves submerged and oriented transversely in aperture, valvular projections directed medially and abutting or overlying each other in midline. Valves (Figs. 28-29) moderately large, subequal, corners extending into moderately long, dactyliform projections, curving toward each other and nearly touching apically. Receptacle large, located dorsolaterad to valves, corners curving partly around operculum. Latter small, located under free, dorsal, end of valves.

*Variation.* — I include under *angularis* all forms in Arkansas, Louisiana, and Mississippi with long acropodites, at least 1/3 of the length of the telopodite, that curve or bend by midlength and whose apertures display divided lateral margins with caudolateral pouches that vary from open to closed. The sides are entire and pouches are absent from *goodi*, whose acropodites curve apically. *Eurymerodesmus angularis* is highly variable in both sexes, and the only plausible alternative is several different species. The situation is analogous to that with the xystodesmid *Deltotaria brimleii brimleii* Causey in the southern Appalachian Mountains, where a host of dissimilar forms, none demonstrating structural stability over a broad geographical area, con-

nect through intermediate populations that bridge the anatomical gaps (Shelley and Whitehead 1986). Intervening forms are unknown in *angularis*, but future collections are expected to show that the localized forms blend together into a single taxonomic unit. A few, such as the falcate form in Union County, Arkansas, may warrant taxonomic recognition as subspecies, but these decisions are left to future investigators with access to more material. The name *wellesleybentoni* Causey (1952a), a cumbersome amalgam of the first and last names of the collector, was proposed for a form from Phillips County, Arkansas, with a stronger acropodal bend, and fortunately can be placed in synonymy.

Variation in males of *angularis* is analyzed geographically from the type locality, beginning with forms to the north and east and proceeding to the south and west. The males from Missouri are nearly identical to the holotypes, but that from IZARD County, Arkansas, a partial specimen, is similar to the one from south of Strong, Union County, Arkansas in possessing a longer, strongly falcate acropodite, which is about 3/4 of the telopodite length. The outer lateral margin in the IZARD County male is lower than the anterior part of the side and does not extend as far laterad thus forming a shallower pouch.

East of the type locality there is a trend toward shorter acropodites beginning with the form named *wellesleybentoni* from Phillips County, where it is subequal to the prefemur and bends more strongly dorsolaterad near midlength (Fig. 22). The outer lateral margin is the same elevation and nearly linear with the anterior part of the sides, and since the inner lateral margin curves, the pouch is comparatively narrow, shallow, and closed (Fig. 21). Farther east in Oktibbeha County, Mississippi, the acropodite is subequal to the prefemur and curves slightly dorso-laterad. The outer lateral margin is lower than the anterior part of the sides and flares moderately laterad, thus forming a moderate, partly open pouch.

Forms south of the type locality exhibit greater variability in both the gonopods and apertures, although those from adjacent Jefferson County closely resemble the types. The acropodites and prefemora are subequal in length in all north-central Louisiana males except those from Ouachita Parish, where the former is much shorter, about 1/3 of the telopodite length and resembles the condition in *compressus*. The acropodite curves slightly dorso-laterad in Morehouse Parish and more directly laterad in the Franklin and Catahoula males. The

outer lateral margin slopes dorsad and flares farther laterad in these specimens thus forming a larger pouch.

Three forms occur in Union County, Arkansas. The males south of Strong display long falcate acropodites, around 3/4 of the telopodite length (Fig. 24), that are convergent with the variant in IZARD County. The bases of the acropodites cross in the midline, then they curl over the outer caudal margin on the opposite side of the aperture and cross the midline and the opposite member again over the sternum between the 9th legs. The outer lateral margin rises from the division point, and the inner lateral margin extends well into the opening, thus forming a deep, open pouch (Fig. 23). The precise locality of the other Union County form is unknown, but the acropodite comprises about half the telopodite length and curves nearly directly dorsad over the sternum between the 9th legs; the prefemur exhibits a distinct distomedial shoulder. The outer lateral margin is level, flares moderately laterad, and forms a moderate pouch with the inner margin.

Forms in southwestern Arkansas and adjacent Louisiana display moderately long acropodites. Those from Columbia County, Arkansas, are subequal to the prefemur, or 1/2 of the telopodite length, and curve distinctly laterad; there is a slight distal shoulder on the prefemur. The outer lateral margin flares farther laterad, and the inner margin curves more into the opening, thus forming a broader and deeper pouch. The Caddo Parish, Louisiana, male has a very long, bisinuate acropodite, but it is only about half the telopodite length because the prefemur is also longer (Figs. 25-26). The telopodite curves strongly laterad, extending into the pouch, and the outer lateral margin is much higher than the anterior parts of the sides. The inner margin curves smoothly into the opening and the inner caudal margin (Fig. 25).

Less can be said about variation in females because most samples contain only males. Females from Franklin and Catahoula Parishes, Louisiana, resemble those from Jefferson County, Arkansas, in having subequal dactyliform projections from the valves that are bowed towards each other and touch in some individuals, thus resembling opposable digits or claspers. The projections are shorter and diverge, extending directly anterior and caudad, in the female from Ouachita Parish, Louisiana (Fig. 30).

*Ecology.* — No habitat comments have appeared in the literature, and the only notation on sample



labels is "leaf mold in woodland" for the sample from Jefferson County, Arkansas.

*Distribution.* — The Coastal Plain of Arkansas and northern Louisiana, extending eastward to eastern Mississippi and northward in Missouri to the fringe of the Ouachita Physiographic Province (Figs. 9, 211). Specimens were examined as follows:

MISSOURI: *Johnson Co.*, Warrensburg, 2M, 2F, 8 April 1962, K. Oyer (FSCA).

ARKANSAS: *Izard Co.*, Mt. Pleasant, M, 23 December 1954, N. B. Causey (FSCA). *Prairie Co.*, DeValls Bluff, M, F, 1 April 1950, L. Gray (ANSP) TYPE LOCALITY. *Jefferson Co.*, 0.5 mi. S. Altheimer, west of AR hwy. 88, 5M, 3F, 14 April 1956, collector unknown (FSCA). *Phillips Co.*, Helena, M, October-November 1951, W. Benton (ANSP), and 20 mi. E Pine Bluff, M, F, October 1954, Kirkwood (FSCA). *Ouachita Co.*, 5 mi. SW Camden, M, F, 1 January 1956, A. B. Jones (FSCA). *Union Co.*, locality unknown, 3M, 8 January 1958, L. O. Warren (FSCA); and south of

Strong, 3M, 19 March 1953, collector unknown (FSCA). *Columbia Co.*, Magnolia, 4M, 28 January 1955, P. Waler (FSCA), M, 19 April 1958, W. F. Evans (FSCA), and 2M, 26 November 1961, R. Rogers (FSCA).

LOUISIANA: *Caddo Par.*, ca. 30 mi. NNW Shreveport, near Myrtis on McCloud-State Line Rd., 0.3 mi. W LA hwy. 1, M, 11 March 1966, R. E. Tandy (FSCA). *Morehouse Par.*, 12 mi. N Bastrop, along LA hwy. 142, 2.1 mi. S AR line, M, 16 March 1967, J. E. and M. R. Cooper (NCSM); and 5 mi. S Mer Rouge, M, F, 24 December 1954, N. B. Causey (FSCA). *Ouachita Par.*, Monroe, 4M, 2 April 1969, collector unknown (FSCA), and 1410 Forsyth Ave, M, 26 April 1976, and F, 31 December 1974, M. R. and J. E. Cooper (NCSM). *Caldwell Par.*, along Lafourche River, 3M, F, date and collector unknown (FSCA). *Franklin Par.*, Winnsboro, M, F, May 1953, M. K. Wiggers (FSCA). *Catahoula Par.*, ca. 17 mi. NE Jonesville, along LA hwy. 15 between Peck and Sicily Island, 3M, 3F, 24 December 1954, N. B. Causey (FSCA); and 4 mi. W Sicily Island, along LA hwy, 8, F, date unknown, R. E. Tandy (FSCA).

MISSISSIPPI: *Oktibbeha Co.*, Craig Springs, M, 22 April 1980, G. Snodgrass (MEM, NCSM).

Remarks. — With known occurrence in the western fringe of Caddo Parish, Louisiana, *angularis* should be expected in Cass and Marion counties, Texas.

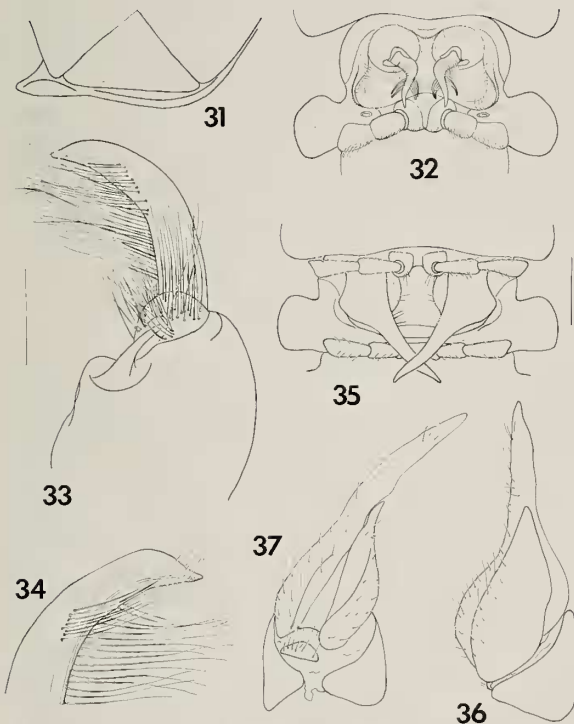
### *Eurymerodesmus compressus* Causey

Figs. 9, 31-37, 211

*Eurymerodesmus compressus* Causey, 1952a:169-171, figs. 1-4. Chamberlin and Hoffman, 1958:79.

*Type specimen.* — Male neotype and one associated female (FSCA) collected by W. Nesbit on an unspecified date in 1957, 6 mi. W El Dorado, Union Co., AR. This site is about 4 mi. N of the type locality, Junction City, Union County, where 16 males and 2 females were collected in October 1950. The types are missing from the ANSP, the published repository (Causey 1952a, Chamberlin and Hoffman (1958), nor is there any material from Junction City in the FSCA. According to Causey (1952a), 1 female topotype was collected at Junction City on 10 May 1950 and 11 males were taken there on 16 January 1952.

*Diagnosis.* — A large species; males characterized by long mandibular projection; sides of aperture divided, with open caudolateral pouches; telopodite moderately long; acropodite moderately long, about



Figs. 31-37. *Eurymerodesmus compressus*. 31, left mandibular projection of neotype, lateral view. 32, aperture and gonopods *in situ* of neotype, ventral view. 33, left gonopod of the same, lateral view. 34, telopodite of the same, medial view. 35, cyphopods *in situ*, ventral view of female from Union Co., AR. 36, left cyphopod of the same, medial view. 37, the same, caudal view. Scale lines for figs. 32 and 35 = 1.00 mm. Line for other figs. = 0.25 mm for 36-37, 0.30 mm for 31, 0.40 mm for 33, and 0.50 mm for 34.

3/8 of telopodite length, broadly terminal, poorly demarcated from prefemur, laterally compressed; prefemur with many hairs arranged continuously along inner margin; cyphopod valves of females with unequal, closely appressed, rigid projections from distal corners, that of outer (lateral) valve very long, dactyliform, overhanging at least segment 4 *in situ*, that of inner (medial) valve much shorter, subtriangular; receptacle moderately large, sides curving partly around operculum.

*Color in life.* — Peritremata orange; metaterga uniformly dark mottled olive, without stripes; collum with orange stripe along anterior margin (Causey 1952a).

*Neotype.* — Length 37.4 mm, maximum width 5.4 mm, W/L ratio 14.4%

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 3.1 mm, interantennal isthmus 1.0 mm. Antennae reaching back to anterior half of 3rd tergite, relative lengths of antennomeres  $2 > 3 > 5 > 4 = 6 > 1 > 7$ . Genae with faint impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, subantennal 1-1, clypeal about 14-14, labral about 20-20. Process of mandibular stipes (Fig. 31) moderately long and broad, apically blunt and rounded.

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-10, becoming progressively more acute caudad.

5th sternum with low, sparsely hirsute areas between 4th legs, narrowly segregated in midline, and strong, sparsely hirsute projections between 5th legs, narrowly segregated in midline; 6th sternum with low, sparsely hirsute elevated areas between both leg pairs, widely separated in midline, those between anterior (6th) legs higher. Postgonopodal sterna with deep central impression between 9th legs; segments 8-9 with low, knob-like projections between both leg pairs, narrowly segregated in midline, those between caudal legs much higher with a few more hairs; segments 10-15 flat between anterior legs, with moderate knob-like projections between caudal legs, becoming progressively smaller caudally with only light hirsute patches on segments 16-18. 2nd coxae with sharply conical anterodistal lobes, caudal lobes absent. Prefemoral lobes present on all legs, becoming smaller on caudalmost segments.

Gonopodal aperture (Fig. 32) broadly trapezoidal, with narrow, open caudolateral pouches and broad anterior indentation, 2.9 mm wide and 1.3 mm long at maxima, outline of apparatus trapezoidal; anterior indentation short, broad, apically rounded; sides divided, angling slightly caudolaterad, elevating just beyond anterolateral corner and continuing to division point at midlength, inner lateral margin plunging deeply into opening then curving broadly into inner caudal margin, outer lateral margin tapering rapidly dorsad, flaring slightly laterad and curving into outer caudolateral corner, forming narrow, open pouch with inner margin, rims essentially smooth; inner caudolateral corner smoothly rounded; outer caudolateral corner generally broadly rounded, somewhat irregular; inner caudal margin curving anteriorly, parallel to outer caudal margin; latter curving broadly anteriorly along anterior surfaces of coxal condyles; margins irregularly hirsute with long hairs arising from rims and outer sur-

faces of sides, slightly more hairs on anterior indentation and moderately dense tufts from pouches, caudal margins glabrous. Gonopods *in situ* (Fig. 32) with telopodites extending caudad in subparallel arrangement, continuing beyond caudal margins of aperture and terminating over coxal condyles, apices directed dorsad. Gonopod structure as follows (Figs. 33-34): Telopodite moderately long, terminating well before distal extremities of hairs. Prefemur moderately long, about 5/8 of telopodite length, curving slightly near midlength and leaning over coxa, margins parallel, not tapering, without distal lobe or swelling, with two rows of long hairs along inner surface angling slightly outward, and distomedial tuft of 8-10 hairs. Acropodite moderately long and broadly terminal, about 3/8 of telopodite length, continuous with, and poorly demarcated from, prefemur, compressed laterally, curving slightly more dorsad, sides tapering rapidly beyond midlength to subacuminate tip.

*Female* — Length 29.6 mm, maximum width 4.5 mm, W/L ratio 15.2%. Agreeing essentially with neotype in somatic features, with following exceptions: Mandibular stipes with short, acuminate, lightly sclerotized projection. Sterna flat, unmodified, with variably impressed transverse grooves originating between leg pairs and at most only a few scattered hairs per segment adjacent to caudal coxae.

Cyphopodal aperture elliptical, sides thickened, strongly elevated above metazonal surface, tapering rapidly to metazonum on caudal margin. Cyphopods *in situ* (Fig. 35) lying obliquely in aperture, open side anteromedial, valvular projections directed caudomedial over caudal margin of aperture, those of outer valves extending over sternum of segment 4, crossing in midline, terminating over prozonum of segment 5. Valves (Figs. 36-37) relatively large, unequal, lateral (outer) valve much larger, situated obliquely on receptacle, inner margins moderately hirsute, outer corners extended into unequal projections, that of inner valve relatively short and subtriangular, closely appressed to inner margin of outer valvular projection, latter very long, more than twice as long as inner projection, rigid, and digitiform, apically acuminate. Receptacle moderately large, glabrous, oriented dorsoventrally in aperture, sides curving broadly around sides of operculum. Latter small, situated directly beneath valves.

*Ecology.* — Unknown.

*Distribution.* — Known only from western Union County, Arkansas (Figs. 9, 211). In addition to Junction City, Causey (1952a) reported a female from Three Creeks, which is also lost. Thus, the neotype and female were the only specimens examined.

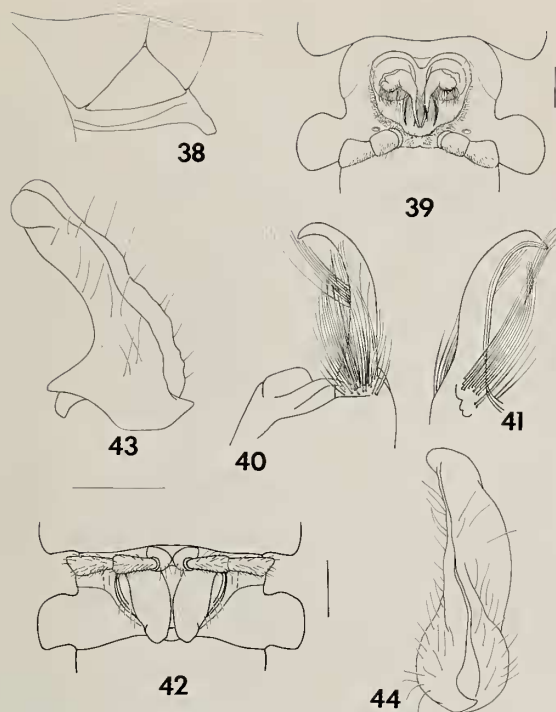
*Remarks.* — With a moderately long acropodite, 3/8 of the telopodite length, *compressus* spans the anatomical gap between the long structures displayed by the rest of the *impurus* group and the short ones, 1/4 of the telopodite length or less, found in the *varius* group, thus blending the dissimilar forms of these groups into one lineage.

### **Eurymerodesmus goodi** Causey

Figs. 9, 38-44, 211

*Eurymerodesmus goodi* Causey, 1952b:3-4, fig. 1. Chamberlin and Hoffman, 1958:79-80.





Figs. 38-44. *Eurymerodesmus goodi*. 38, right mandibular projection of holotype, lateral view. 39, aperture and gonopods *in situ* of male from Montgomery Co., AR, ventral view. 40, left gonopod of holotype, lateral view. 41, telopodite of the same, lateral view. 42, cyphopods *in situ*, ventral view of female from Polk Co., AR. 43, left cyphopod of the same, subcaudal view. 44, the same, anterolateral view. Scale lines for figs. 39 and 42 = 1.00 mm. Line for other figs. = 0.30 mm for 38 and 43-44, and 0.50 mm for 40-41.

*Type specimen.* — Male holotype (AMNH) collected by N. B. Causey, 7 September 1950, along Bard Springs Rd., 16 mi. SE Mena, Polk Co., AR.

*Diagnosis.* — A large species; males characterized by long mandibular projection; sides of aperture undivided, without caudolateral pouches, elevating slowly throughout, without modifications; telopodite long; acropodite long, about 2/3 of telopodite length, broadly terminal, moderately demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners extending into long, broad projections; receptacle absent.

*Color in life.* — Peritremata reddish-orange; dorsum olive, darker on prozonites, lighter on metazonites; without metatergal stripes (Causey 1952b).

*Holotype.* — Body fragmented, length unmeasurable, maximum width 5.8 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 3.7 mm, interantennal isthmus 1.1 mm. Antennae reaching back to middle of 3rd tergite, relative

lengths of antennomeres  $2 > 5 > 4 = 6 > 3 > 1 > 7$ . Genae without impressions. Facial setae as follows: epicranial absent, interantennal 1-1, frontal 1-1, genal absent, clypeal about 11-11, labral about 20-20. Process of mandibular stipes long, angling caudad, apically blunt (Fig. 38).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded on anterior half of body, becoming blunt and progressively more acute on caudalmost segments.

5th sternum with short broad knob-like projections between both leg pairs; 6th sternum with broader, flatter elevated areas between both pairs of coxae. Postgonopodal sterna with slightly elevated, flattened areas between 9th legs; remaining sterna with hirsute, elevated areas on segments 8-10, becoming progressively flatter and less hirsute caudad, with incomplete transverse impressions originating between leg coxae. 2nd coxae with broad, truncate anterodistal lobe and shorter, acute caudal one. Prefemoral lobes present on all legs, becoming smaller on caudalmost segments.

Gonopodal aperture (Fig. 39, not this specimen) very wide, broadly ovoid, without caudolateral pouches, strongly indented anteriorly at midline, 3.6 mm wide and 1.7 mm long at maxima; anterior indentation strong, broadly rounded; sides not divided, curving medially caudally, elevation beginning behind anterolateral corner, continuing to peak at caudolateral corner, rims essentially smooth; caudolateral corner broadly rounded, obtuse; caudal margin continuous with sides at caudolateral corners, dropping abruptly to metazonal surface and continuing across midline; anterior margin glabrous, hairs beginning on sides behind anterolateral corners, becoming progressively denser caudad, arising from rim or slight distance down outer surface, densest at caudolateral corners, continuing along midline of caudal margin in linear arrangement. Gonopods *in situ* (Fig. 39, not this specimen) with telopodite angling caudomedially, apices nearly touching, located wholly within aperture. Gonopod structure as follows (Figs. 40-41): Telopodite relatively long, terminating before level of distal extremities of hairs. Prefemur short, about 1/3 of telopodite length, expanding distad and terminating in swollen area, with two rows of hairs along inner margin and distomedial tuft of about a dozen hairs. Acropodite long and broadly terminal, about 2/3 of telopodite length, moderately demarcated from prefemur, linear for most of length, curving broadly distal to midlength, sides tapering gradually then more rapidly apically, tip subacuminate.

*Female from Polk Co.* — Length 29.6 mm, maximum width 4.8 mm, W/L ratio 16.2%. Agreeing closely with holotype in somatic features, with following exceptions: Genal setae 1-1. Process of mandibular stipes short, blunt. Sterna relatively flat and unmodified, with faint, incomplete transverse impressions originating between coxae and at most only a few randomly scattered setae, especially along caudal margins.

Cyphopodal aperture ovoid, caudal margin extending caudad in midline, sides and caudal margin distinctly elevated above metazonal surface, caudal margin strongly flared, overhanging segment margin. Cyphopods *in situ* (Fig. 42) with ventral extensions of valves protruding through aperture, directed caudad, overhanging caudal margin of aperture and coxae of 3rd legs, open side visible, facing sublateral. Valves (Figs. 43-44) large, moderately hirsute, slightly unequal, dorsal one with short, broad process curving over opening between valves, distal corners extending into long broad projections, longer than main part of valves, leaning dorsad, narrowing then expanding into rounded, knob-like termini. Receptacle absent. Operculum minute, tucked under anterior side of valves.

*Variation.* — Measurements of the male from Montgomery County illustrated in Figs. 39-41 are 32.5 mm in length, 5.3 mm in width, W/L ratio 16.3%. Its gonopods agree closely with those of the holotype, but the caudal aperture margin extends caudad between the 8th legs to near the sternal elevations.

*Ecology.* — Unknown.

*Distribution.* — Known only from southwestern Polk and southwestern Montgomery counties, Arkansas, in the southern fringe of the Ouachita Physiographic Province (Figs. 9, 211). Specimens were examined as follows:

ARKANSAS: *Polk Co.*, along Bard Springs Rd., 16 mi. SE Mena, M, 7 September 1950, N. B. Causey (AMNH) TYPE LOCALITY; and Shady Lake Rec. Area, M, F, 18 June 1953, D. Dowling (FSCA). *Montgomery Co.*, 10 mi. NW Langley (in Polk Co.), Albert Pike Cpgd., M, F, 1979, H. W. Robison (NCSM) and M, 24 December 1982, H. W. Robison (NCSM).

*Remarks.* — *Eurymerodesmus goodi* is a relatively soft, flexible eurymerodesmid, and its large size is equivalent to that of moderately-large xystodesmids such as *Boraria profuga* (Causey), also occurring in Arkansas. Because of its size *goodi* is particularly likely to be misassigned to the Xystodesmidae, and close attention should be paid to the structures of the mandibular stipes and leg prefemora when making determinations.

### The Dubius Group

*Eurymerodesmus dubius* shares a wide aperture lacking caudolateral pouches with *goodi*, which is parapatric on the north. It differs in having a short acropodite and short, mostly linear telopodites, the latter distinguishing it from other members of the *Kewanius* lineage. It differs from the species of the *varius* group in the linear telopodite and the absence of caudolateral pouches, and is distinguished from those in the *simplex* group by its broadly terminal acropodite.

*Component.* — *dubius* Chamberlin.

### *Eurymerodesmus dubius* Chamberlin

Figs. 9, 45-53, 211

*Eurymerodesmus dubius* Chamberlin, 1943:38, fig. 8; 1952:573. Causey, 1952b:2-3. Chamberlin and Hoffman, 1958:79.

*Paresmus columbus* Causey, 1950a:272, figs. 10-11. Chamberlin and Hoffman, 1958:82. NEW SYNONYMY.

*Type specimens.* — Male holotype and female paratype (FMNH) collected by K. P. Schmidt, 16 April 1941, at Delight, Pike Co., AR.

*Diagnosis.* — A large species; males characterized by short mandibular projection; sides of aperture undivided, without caudolateral pouches, elevating slowly, without modifications; telopodite short, nearly upright for most of length; acropodite short, 1/8 to 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, gently curved; prefemur with many hairs arranged continuously along inner surface; cyphopod valves of females with distal corners only slightly extended; receptacle absent.

*Color in life.* — Unknown. Chamberlin's description (1943) indicates a stripe across the caudal margins of the metaterga, but the living colors cannot be inferred from those in preservative.

*Holotype.* — Body highly fragmented, length unmeasurable, maximum width 5.8 mm.

Somatic features similar to *hispidies*, with following exceptions:

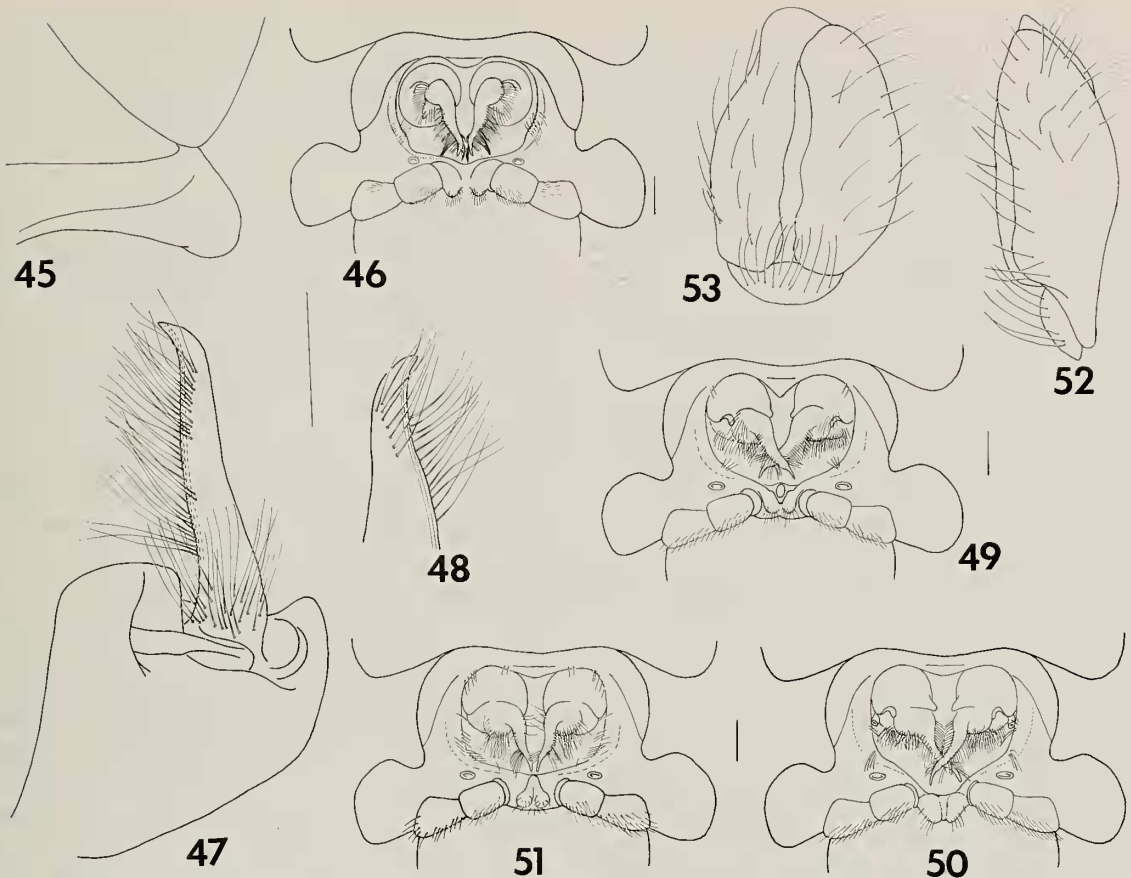
Width across genal apices 3.6 mm, interantennal isthmus 1.0 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres  $2 > 6 > 3 = 4 = 5 > 1 > 7$ . Genae with distinct, central impressions. Facial setae as follows: epicranial, interantennal, and frontal absent; genal 1-1, clypeal about 9-9, labral about 16-16. Process of mandibular stipes short and stout, apically broadly rounded (Fig. 45).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-14, becoming progressively more acute caudally.

5th sternum with short projections between anterior legs, closely appressed in midline, and broader, more widely segregated, knob-like processes between caudal legs; 6th sternum with short, knob-like projections between anterior legs and broad, flattened, areas between caudal legs. Postgonopodal sterna with short, broad lobes between 9th legs; sternum of segment 8 deeply incised transversely, with hair patches adjacent to leg coxae; remaining sterna becoming flatter and more plate-like caudally, with hair patches adjacent to leg coxae through segment 17, becoming progressively less hirsute caudad. 2nd coxae with short distal lobes on anterior and caudal surfaces. Prefemoral lobes extending through segment 12.

Gonopodal aperture (Fig. 46) nearly circular, without caudolateral pouches, with slight anterior indentation, 2.0 mm wide and 1.4 mm long at maxima; anterior indentation short and broad, apically rounded; sides curving gently caudomedial, undivided, elevating slightly to peak just before caudolateral corner, then dropping abruptly to metazonal surface, rims becoming slightly irregular caudad; caudolateral corner moderately blunt, sloping downward to metazonal surface; caudal margin not continuous with and much lower than lateral, extending slightly caudad in midline; anterior and caudal margins glabrous, sides with only a few scattered hairs on rim and outer surface near peak at caudolateral corners. Gonopods *in situ* (Fig. 46) angling toward midline with tips nearly touching, telopodites located wholly over aperture. Gonopod structure as follows (Figs. 47-48): Telopodite relatively short and upright, terminating well before level of distal extremities of hairs. Prefemur relatively long, about 7/8 of





Figs. 45-53. *Eurymerodesmus dubius*. 45, right mandibular projection of holotype, lateral view. 46, aperture and gonopods *in situ* of holotype, ventral view. 47, left gonopod of the same, lateral view. 48, telopodite of the same, medial view. 49, aperture and gonopods *in situ* of male from Bradley Co., AR, ventral view. 50-51, apertures and gonopods *in situ*, ventral views of two males from Clark Co., AR. 52, left cyphopod of female paratype, medial view. 53, the same, anterior view. Scale lines for figs. 46 and 49-51 = 1.00 mm. Line for other figs. = 0.35 mm for 45, 0.40 mm for 47, and 0.50 mm for 48 and 52-53.

telopodite length, upright but not linear, margins slightly bisinuate curved, narrowing slightly distad, basal hairs relatively sparse, hairs denser on stem, with two rows along inner margin angling outward distad and terminating in tuft of about 12 hairs, with distomedial tuft of 8 hairs. Acropodite very short, broadly terminal, about 1/8 of telopodite length, covered by prefemoral hairs, essentially just a short spur on distal extremity of prefemur, continuous with, and poorly demarcated from, latter, curving gently dorsad, sides tapering to acuminate tip.

*Female paratype.* — Body fragmented, length unmeasurable, maximum width 4.8 mm. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal and frontal setae present, 1-1 each; genal setae absent. Process of mandibular stipes indistinct, broadly rounded. Sterna relatively flat, unmodified, with at most only a few randomly scattered hairs on caudal margins.

Cyphopodal aperture small, circular, sides and caudal margin nearly flush with metazonal surface. Cyphopods *in situ* with tips of valves visible in aperture, not protruding, open side directed anteriorly. Valves (Figs. 52-53) moderate-size, moderately hirsute, slightly unequal, outer (lateral) valve larger, distal corners very slightly extended, broadly rounded. Receptacle absent. Operculum relatively large, moderately hirsute, located at bases of valves on open (anterior) side.

*Variation.* — *Eurymerodesmus dubius* is one of the more flexible eurymerodesmids, and it was possible to uncoil without breakage and measure males from the counties in Table 4:

Table 4. Size variation of *E. dubius* males.

County	length	width	W/L ratio
Saline	37.8	6.4	1.69%
Garland	33.6	5.6	16.7%
Garland	33.6	5.6	16.7%
Montgomery	32.5	5.3	16.3%
Clark	25.0	4.7	18.8%
Clark	32.7	4.7	14.4%
Pike	34.3	5.5	16.0%
Pike	30.8	4.7	15.3%
Pike	33.6	5.6	16.7%
Pike	29.3	5.3	18.1%
Pike	31.6	5.5	17.4%
Pike	29.8	4.9	16.4%
Nevada	27.5	4.8	17.5%
Bradley	32.5	6.4	19.7%

Aside from one male from Clark County that lacks the distomedial tuft of prefemoral hairs, the gonopods of *dubius* are uniform. However, the *in situ* configuration varies depending upon the degree of coiling of the body, the degree to which the coxae are submerged under the lateral margins of the aperture, and the caudal configuration of the latter. Thus, the apices of the telopodites may be very close, touch, or cross, and they may be wholly within the aperture or slightly overlap the caudal rim. In one tightly coiled male, the aperture was nearly completely covered by segment 6, and the telopodites were correspondingly reoriented, being directed mediad with the apices extending across the opposite side of the aperture and the tips touching the opposing coxae.

As discussed by Causey (1952b), the aperture configuration and the size and shape of the sternal process(es) between the 9th legs vary considerably. The height and length of the lateral elevations varies, and they may be nearly linear or broadly curved. In northern populations, the lateral elevations extend around the caudolateral corners onto the caudal margin, where they terminate either abruptly or smoothly by tapering to the metazonal surface. However, in the southernmost populations from Nevada, Ouachita, and Bradley counties, the elevations are limited to the sides, terminating either at or just before the caudolateral corners.

The caudal margin displays two configurations. It is essentially straight as in the holotype in males from Saline, Garland, and Nevada counties, and in these individuals, the sternal projections between the 9th legs are separate, short, and knob-like, terminating well below the margins of the adjacent coxae. However, in some males from Montgomery, Clark, Pike, Ouachita, and Bradley counties, the margin extends caudad in the midline between the 9th legs terminating at, and tapering into, the sternal projection (Figs. 49-50). Coupled with the anterior indentation, the aperture in these individuals appears heart-shaped. In specimens from Montgomery, Pike, and Bradley counties, the sternal knobs are shorter than the adjacent coxal widths and are separated to varying degrees, either directed ventrad or leaning slightly toward the midline. However, in males from Clark and Ouachita counties, the knobs are coalesced in the midline to form a single ventral projection of varying length (Figs. 50-51). It is longer than the adjacent coxal widths in one male from Clark County (Fig. 50). As a further complication, a short midcaudal spur extends anteriad inside the aperture in a few males from Ouachita and Bradley counties

(Fig. 49). None of these variants demonstrates enough consistency or enough of a geographical component to warrant taxonomic recognition at the subspecific level. However, they emphasize the need to examine every specimen; males within some samples differ.

The cyphopods generally resemble those of the female paratype and protrude through the aperture in a few individuals. In one from Garland County, the valves are oriented laterad/mediad, with the open side facing forward.

*Ecology.* — Labels with specimens from Bradley County state that they were taken in "large traps" in pine-oak woods.

*Distribution.* — The southern fringe of the Ouachita and the adjacent Coastal Plain Physiographic Provinces of southern Arkansas, with an allopatric record from Louisiana (Figs. 9, 211). Specimens were examined as follows:

ARKANSAS: *Montgomery Co.*, along US hwy. 270, 5.4 mi. E Mt. Ida, M, 6 March 1977, R. E. Woodruff (FSCA). *Garland Co.*, Hot Springs, 3M, F, 4 January 1957, collector unknown (FSCA); and Big Goat Island, Lake Hamilton, M, 28 December 1954, Atkins (FSCA). *Hot Springs Co.*, Magnet, F, 1880's but exact date unknown, Hutcherson (NMNH). *Saline Co.*, locality unknown, 2M, 2 juvs., 1950, N. B. Causey (FSCA). *Clark Co.*, 4.5 mi. N Arkadelphia, M, 19 January 1953, and 4M, February 1953, J. E. Sublette (FSCA); 4 mi. E Arkadelphia, M, F, date and collector unknown (FSCA); and 8 mi. W Arkadelphia, 3M, 2F, 10 September 1950, collector unknown (FSCA). *Pike Co.*, Delight, M, F, 16 April 1941, K. P. Schmidt (FMNH) TYPE LOCALITY; and Bear Cr., 7M, 2F, 18 April 1954, N. B. Causey (FSCA). *Nevada Co.*, Jackson Twp., 5M, 3F, 30 December 1954, R. Delaney (FSCA). *Ouachita Co.*, 5 mi. SW Camden, M, 27 November 1955, A. B. Jones (FSCA). *Bradley Co.*, Prospect, 3M, 29 November 1967, Whitcomb (FSCA); and Sumpter, 2F, September and 13 October 1965, and 3M, 21 and 28 December 1964, L. Whitcomb (FSCA).

LOUISIANA; *Catahoula Par.*, Sicily Island (not town), 2M, 2F, 2 juvs., 12 October 1974, S. Ziser (FSCA).

In addition to these specimens, the record from Dallas County, Arkansas, locality not specified (Causey 1952b), is considered valid and is so indicated in figures 9 and 211. There is also an Arkansas sample in the FSCA containing two males, six females, and six juveniles from an unspecified location in Washington County. This site is so distant



from the others that I think it may represent a labeling error and prefer to omit it. For many years Dr. Causey's home was in Washington County, where she and others collected many eurymerodesmids. If *dubius* does occur there, I think it would have been collected more than once.

Since Causey's sketch of the gonopod of *Paresmus columbus* (1950a, fig. 11) closely resembles that of *dubius*, I include *P. columbus* in the synonymy and show its type locality, 3 miles east of Magnolia, Columbia County, Arkansas, as a literature record (Figs. 9, 211). The type series of *P. columbus* contained the male holotype and a female allotype, both of which are missing from the ANSP, the reported repository (Causey 1950a, Chamberlin and Hoffman 1958). No other localities have been recorded for *P. columbus*.

*Remarks.* — *Eurymerodesmus dubius* is one of the more flexible congeners, hence the large number of measurements since it was possible to uncoil many males without breakage. Like *goodi*, *dubius* may be confused with xystodesmids because of its large size. The relatively linear, upright telopodites are superficially similar to those of *digitatus* (compare figs. 47-48 and 199-200), a resemblance attributable to convergence. Likewise, their enclosure within the aperture is convergent with the condition in the *melacis* lineage.

The Louisiana locality is about 100 miles from the closest known site in Arkansas. Field work is therefore needed in northern Louisiana to determine whether these areas connect.

### The Varius Group

The *varius* group is characterized as follows: apertures with divided lateral margins and caudolateral pouches; acropodites short, no more than 1/4 of the telopodite length, broadly terminal, and poorly demarcated from the prefemur at least in some populations of each component species; prefemora long, at least 3/4 of telopodite length, without distinct terminal lobes on outer surfaces in all populations. The subspecies of *varius* in southwestern Louisiana between the Pearl and Mississippi Rivers, *v. christianus*, possesses strong terminal prefemoral lobes that clearly demarcate the acropodite. However, this trait is not shared by all races of *varius*. The nominate subspecies, in the southeast along the Atlantic Coast, and some forms of *v. louisianae* in northern Louisiana lack distinct lobes, and the acropodite is therefore continuous with the prefemur. Other species have at most a

slight lobe or swelling, so the key feature of the *varius* group is the absence of the lobe from some populations of each species. Since the *simplex* group contains forms with strong prefemoral shoulders and subterminal or narrowly terminal acropodites, *varius* itself bridges the anatomical gap between the two groups through its lobed forms. The two groups could therefore be combined, but it is convenient to segregate them based on the acropodal feature. The *varius* group covers nearly all of the range of the *Kewanius* lineage, extending from the Atlantic Ocean to eastern Texas, east-central Missouri, and southern Illinois, with an apparently allopatric population in Mason County, Texas (Figs. 213). The only regions that it does not encompass are the area occupied by *impurus*, Brazos and Washington counties, Texas, and west-central Missouri.

*Components.* — *varius* (McNeill) [*v. varius*, *v. christianus* Chamberlin, *v. louisianae* Chamberlin]; *newtonus* Chamberlin; *oliphantus* Chamberlin; *amplus* Causey; *elevatus*, new species.

### *Eurymerodesmus varius* (McNeill)

*Diagnosis.* — A small to moderate-size species; males characterized by variable mandibular projection, ranging from minute, nubbinlike, and subequal to that of females to moderate-size; sides of aperture divided, with closed caudolateral pouches; telopodite long; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly to sharply demarcated from prefemur; latter with or without rounded distal lobe on outer margin, with relatively few hairs arranged sporadically and discontinuously along inner surface; cyphopod valves of females with distal corners extending into angular ridge, angling toward corner; receptacle moderate-size, sides not curving around operculum.

*Remarks.* — The third oldest species in the family, *varius* occupies the largest distribution, covering the entire area east of the Mississippi River, with scattered, possibly relictual populations in north-central Louisiana and southern Arkansas (Fig. 54). The distal end of the gonopod prefemur undergoes an east-west clinal change ranging from either no, or only a slight, distal prefemoral swelling in populations along the Atlantic and Gulf Coast westward to western Alabama, to a somewhat larger swelling in those in Mississippi, to a strong, broadly rounded lobe in ones in southeastern Louisiana between the Pearl and Mississippi Rivers, to a variably small to moderate-size swelling in forms in northern Louisiana and Arkansas. As the swelling becomes larger,

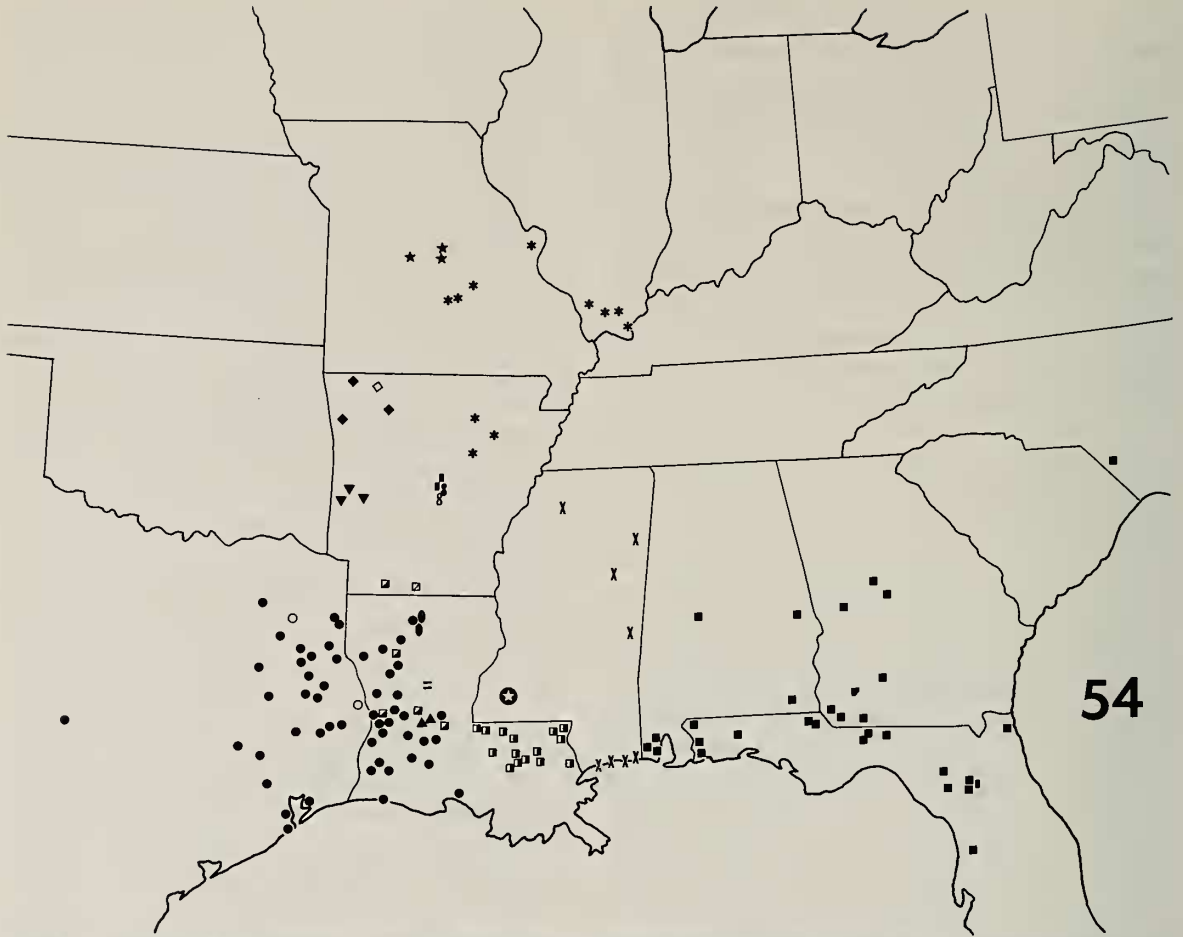


Fig. 54. Distributions of the *varius* and *simplex* groups. Squares, *varius varius*; X's, *varius* intergrades; vertical half-shaded squares, *varius christianus*; diagonal half-shaded squares, *varius louisianae*; dots, *amplus*; diamonds, *newtonus*; asterisks, *oliphantus*; stars, *elevatus*; upright triangles, *simplex*; inverted triangles, *polkensis*; star in dot, *caesariatus*; ovals, *paroicus*; equals sign, *crassatus*; 8's, *pulaski*; and rectangles, *serratus*. Open symbols denote literature records considered valid.

the acropodite becomes correspondingly more sharply demarcated, and in populations in southeastern Louisiana the latter is discontinuous with the prefemur, thereby resembling the condition in *simplex*. Most Atlantic populations exhibit a trace of a swelling, but a few lack this and have parallel-sided prefemora, such as that at the type locality, Pensacola, Escambia County, Florida. Accompanying these gonopodal changes is variation in the mandibular projection. All males from east of the Mississippi River display minute, rounded, and weakly sclerotized processes, at most only slight nubbinlike vestiges or rounded lobes subsimilar to those in females. The projection is larger and variable west of this boundary, being subtriangular and apically sub-acuminate in some males and still larger, more heavily sclerotized, and apically blunt or truncate in others. All forms possess sparsely and sporadically hirsute prefemora indicative of a single species, but

the clinal changes in the distal prefemoral swelling and those involving the mandibular process are significant enough to justify taxonomic recognition at the subspecific level. Since the type locality is in the east, in the area occupied by forms with only slight swellings, they become the nominate subspecies, and *louisianae* Chamberlin was proposed for those in northern Louisiana and southern Arkansas with larger mandibular projections. No name is available for the lobed population in southeastern Louisiana, but *christianus* Chamberlin was proposed for an intergrade form with an intermediate swelling from Harrison County, Mississippi, only about 35 miles to the east. As first reviser, I conserve this name and assign it to the lobed population. At the Pearl River, the increase in size of the lobe is sharp and dramatic, but the change is more gradual to the east and appears to begin in Mississippi. Consequently, I consider the forms in this state as in-



KEY TO SUBSPECIES, BASED ON ADULT MALES

1. Projection of mandibular stipes weakly sclerotized, a rudimentary nubbin or short, rounded lobe, subsimilar to condition in females (Fig. 55)..... *varius louisianae* Chamberlin
2. Projection larger, heavily sclerotized, subtriangular to blunt and truncate (Figs. 66-67)..... *varius varius* (McNeill)
- Gonopod prefemur with at most only a low, rounded distal swelling, only slightly elevated above outer surface; acropodite poorly demarcated (Figs. 57-58)..... *varius varius* (McNeill)
- Prefemur with distinct terminal lobe, strongly elevated above outer margin; acropodite sharply demarcated (Fig. 65)..... *varius christianus* Chamberlin

tergrades between *v. christianus* and the nominate subspecies, occurring from Alabama eastward. Triangular and blunt mandibular projections are intermixed in northern Louisiana and southern Arkansas, the area occupied by *v. louisianae*.

The clinal change in *varius* from parallel-sided to lobed individuals is significant because it links the continuous, broadly terminal, and poorly demarcated acropodal forms clearly assignable to *Eurymerodesmus* to the narrowly terminal, strongly demarcated, and discontinuous acropodite of *simplex*, type species of *Kewanius*, which in turn bridges the anatomical gap to the subterminal acropodal forms assignable to *Paresmus*. Consequently, this clinal change provides the necessary evidence to synonymize the last two genus-group names with *Eurymerodesmus*. *Eurymerodesmus varius* is thus an intermediate species connecting all these forms into a single assemblage, but for convenience and ease of comprehension, I divide it into two groups based on poorly or sharply demarcated acropodites. Since this structure is continuous in most populations, *varius* is the oldest available name for the poorly demarcated form and is therefore used to designate this species group.

There are several very large samples of the nominate subspecies, *v. christianus*, and some sizeable ones of intergrades, particularly those taken in pitfall traps. I could also have collected scores of individuals at the North Carolina, and Alachua and Gilchrist counties, Florida, sites. These numbers suggest that studies on population structure and ecology of *varius* would be fruitful.

***Eurymerodesmus varius varius* (McNeill), new status**  
Figs. 54-61

*Polydesmus varius* McNeill, 1887:323-324.

*Leptodesmus varius*: Bollman, 1888b:344.

*Eurymerodesmus minimus* Loomis, 1943:320, fig. 2.

*Eurymerodesmus varius*: Causey, 1954:67. Chamberlin and Hoffman, 1958:81.

*Type specimen*. — Female holotype (NMNH) collected by C. H. Bollman, March-April 1886, at Pensacola, Escambia Co., FL. The original descrip-

tion (McNeill 1887) indicates that the type series contained three females, but the other two are lost. Housed with the holotype is a vial labeled "*Lep-todesmus varius* McNeill, type specimen," containing a male of this form supposedly collected at an unknown site in Indiana. The source of this specimen is unknown, but it is not part of the type series and represents a labeling error since no authentic Indiana localities are known for a eurymerodesmid. It is ignored in this study.

*Diagnosis*. — A small subspecies; males with projection of mandibular stipes minute, nubbinlike, indistinct; acropodite essentially smoothly continuous with, and poorly demarcated from, prefemur; latter with at most only a slight suggestion of distal swelling, weakly elevated above margin.

*Color in life*. — Peritremata pink; metaterga mottled brownish olive with narrow pink stripes along caudal edges connecting peritrematal markings; collum with pink stripes along both anterior and posterior margins. Loomis (1943) described the living color as "translucent white with a light pinkish tinge," which fades rapidly in alcohol.

*Male topotype*. — Length about 14.2 mm, maximum width 1.8 mm, W/L ratio 12.7%.

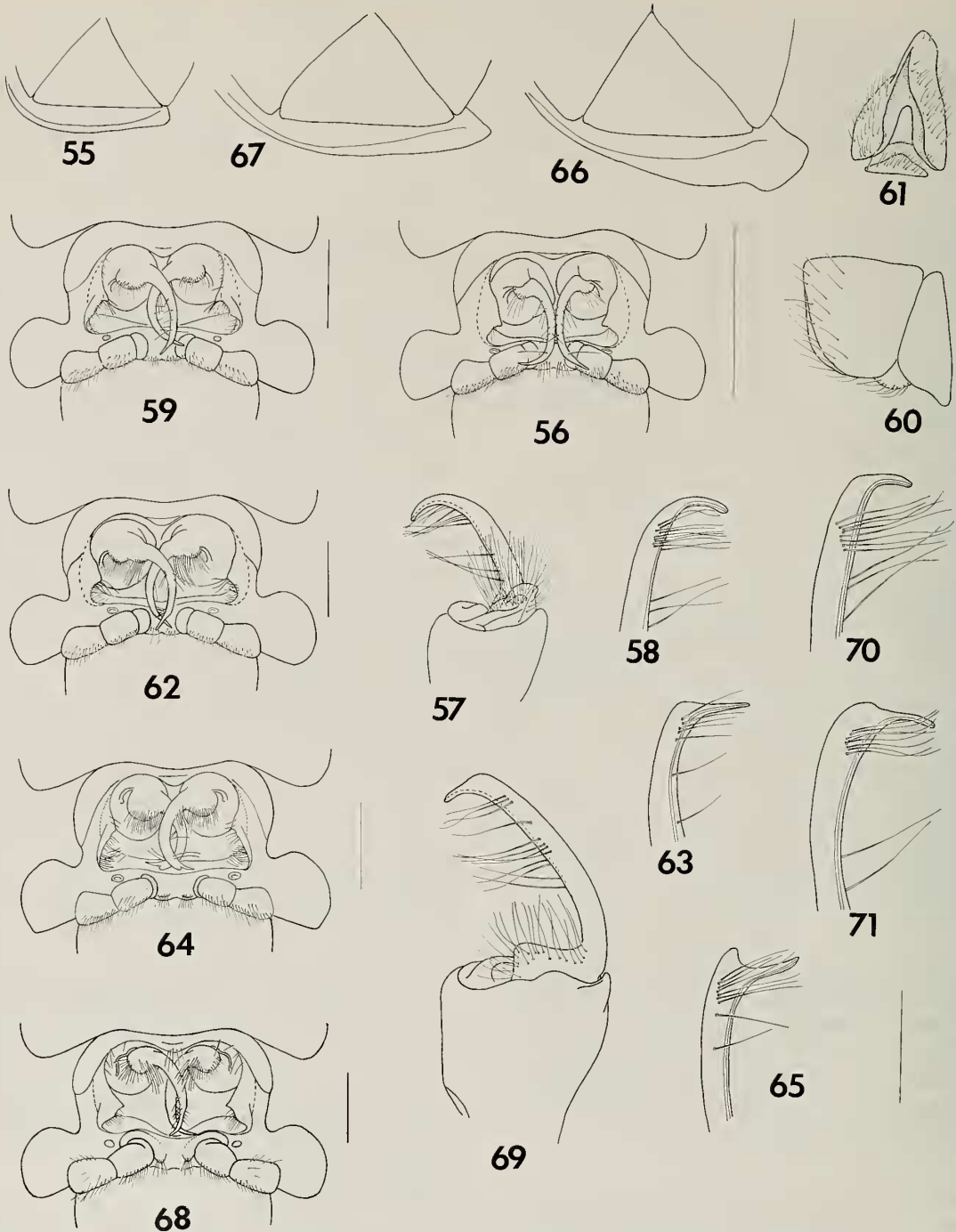
Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 1.3 mm, interantennal isthmus 0.4 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres 2 > 3 > 4 = 5 = 6 > 1 > 7. Genae without impressions. Facial setae as follows: epicranial and subantennal absent, interantennal 1-1, frontal 1-1, genal 3-3, clypeal about 10-10, labral about 14-14. Mandibular stipes with minute, vestigial projection, corner rounded, of general size and configuration as that of female eurymerodesmids, subsimilar to females of *varius* (Fig. 55).

Collum extending slightly below ends of following tergite. paranota depressed, continuing slope of dorsum; posterior corners rounded through segment 7, blunt on 8-13, becoming progressively more acute caudad.

5th and 6th sterna without elevations, with moderate hair patches adjacent to leg coxae. Postgonopodal sterna with minute hirsute lobes between 9th legs, remaining sterna flat and unmodified, with faint transverse grooves and sparse hair patches disappearing in midbody region, caudal sterna glabrous. 2nd coxae without projections. Prefemoral lobes relatively small, restricted to pregonopodal legs.

Gonopodal aperture (Fig. 56) broadly rectangular, with variable caudolateral pouches, slightly indented anteriorly at midline, 1.0



Figs. 55-71. *Eurymerodesmus varius*. 55-61, *varius varius*. 55, projection of right mandible of topotype, lateral view. 56, aperture and gonopods *in situ* of topotype, ventral view. 57, left gonopod of the same, lateral view. 58, telopodite of the same, medial view. 59, aperture and gonopods *in situ* of male from Robeson Co., NC, ventral view. 60, left cyphopod of holotype, caudal view. 61, the same, medial view. 62-63, *varius intergrades*. 62, aperture and gonopods *in situ* of male from Harrison Co., MS, ventral view. 63, telopodite of left gonopod of the same, medial view. 64-65, *varius christianus*. 64, aperture and gonopods *in situ* of male from Washington Par., LA, ventral view. 65, telopodite of left gonopod of male from Ascension Par., LA, medial view. 66-71, *varius louisianae*. 66, right mandibular process of holotype, lateral view. 67, right mandibular process of paratype, lateral view. 68, aperture and gonopods *in situ* of holotype, ventral view. 69, left gonopod of the same, lateral view. 70, telopodite of the same, medial view. 71, telopodite of left gonopod of male from Columbia Co., AR, medial view. Scale lines for figs. 56, 59, 62, 64, and 68 = 1.00 mm. Line for other figs. = 0.40 mm for 55, 66-67, and 69; 0.50 mm for 57-58, 60-61, 63, 65, and 70-71.



mm wide and 0.5 mm long at maxima, outline of apparatus slightly trapezoidal; anterior indentation minute, broadly rounded, barely perceptible; sides angling progressively mediad, leaning over aperture, and becoming progressively more elevated to division point located caudad over caudal margins, inner lateral margin plunging into opening and curving into inner caudal margin, obscured by lean of flare and outer lateral margin, latter leaning strongly mediad but angling laterad and dropping to metazonal surface at caudolateral corner, forming closed pouch with inner margin, rims essentially smooth; inner caudolateral corner smoothly curved, obscured by lean of flare; outer caudolateral corner rounded; inner caudal margin curving gently and bisinuate, subparallel to outer caudal margin; latter flush with metazonal surface, angling slightly caudad in midline; margins glabrous except for slight hair tufts in cavity. Gonopods *in situ* (Fig. 56) with telopodites curving mediad, touching opposite member in midline, then curving broadly laterad, extending well beyond aperture and terminating over coxae or prefemora of 9th legs. Gonopod structure as follows (Figs. 57-58): Telopodite relatively long, terminating at about level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, sides parallel for most of length, narrowing slightly and curving distad, with only 3-4 widely separated hairs on inner margin of proximal part of stem and distomedial tuft of 9 moderately separated hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, smoothly continuous with, and poorly demarcated from, prefemur, continuing broad dorsolateral curvature of latter, narrowing rapidly to subacuminate tip.

*Female Holotype*. — Body fragmented, length unmeasurable (15 mm according to McNeill (1887) ), maximum width 1.7 mm, W/L ratio 11.3%. Agreeing closely with male topotype in somatic features, with following exceptions: Genal setae 1-1. Segments 3-8 with moderate elevations lateral to legs, highest on segments 3-4. Sterna glabrous, flat and unmodified, with incomplete transverse impressions originating between leg coxae.

Cyphopodal aperture elliptical, sides strongly elevated above metazonal surface. Cyphopods *in situ* with distal edges of valves visible in aperture, open side facing dorsad. Valves (Figs. 60-61) relatively large, subequal, completely filling respective sides of aperture, moderately hirsute, distal corners extending ventrad into distinct ridge, bluntly angular at corners. Receptacle moderate in size, glabrous, located laterad to valves, corners not extending partly around operculum, hidden internally under side of aperture. Operculum minute, located under open, dorsal side of valves.

*Variation*. — The Escambia County males agree closely with each other, the only exception being slight differences in the slope of the flare, or outer lateral margin, of the aperture. When the angle of slope is greater, the aperture extends farther laterad and the caudal edge is folded, as shown by a North Carolina male (Fig. 59). The slope of the flare also affects the size and shape of the pouch, and the degree to which it is open or closed; the cavity is narrower and more closed in males with more gradual slopes. The corner of the division point, the highest point on the sides, extends inward and downward or dorsad in males throughout the range.

The gonopods vary in the distance they project caudad, which is a measure of how tightly the body is coiled. Normally, they overhang the sternum be-

tween the 9th legs or the adjacent coxae, but occasionally they extend over more of segment 8. In more tightly coiled specimens, the 6th metazonite may extend over as much as half of the aperture. Topotypical males from Escambia County lack any trace of a distal prefemoral swelling, but most individuals from Georgia, Florida, North Carolina, and Alabama display a suggestion of an enlargement.

*Ecology*. — Causey (1954) collected this subspecies under live oaks in Escambia County, Florida. Habitat notations on vial labels include the following: in house on floor (Alachua Co., FL), under logs (Grady Co., GA), in roadside stream (Okaloosa Co., FL), in pine hardwood litter (Monroe Co., GA), and under horse dung (Gilchrist Co., FL). The samples from Tall Timbers Research Station, Leon County, and Big Bend Horticultural Lab, Jefferson County, Florida, were recovered from pitfall traps, and in at least one sample from the latter site, the trap was under a pecan tree.

In North Carolina, *v. varius* is plentiful at a rural residence in Robeson County, the only known site of eurymerodesmids in the state. They occur under pine and oak logs and in pine litter under azaleas and sesanqua bushes. I thought that this population might be introduced, but the family has resided there for over 20 years, and the shrubs were present when they came. Consequently, this seems a natural population, suggesting that *v. varius* will eventually be found at other sites in southeastern North Carolina and also in coastal South Carolina, where it has not been encountered. This population probably is not the source of the *Eurymerodesmus* sp. or "*Leptodesmus hispidipes*" records from Duke Forest, Durham County (Brimley 1938, Causey 1940, Wray 1967), which I (1978) deleted from the North Carolina fauna, since Causey's illustration (1940, fig. 8) is of a species with continuous prefemoral hairs. Thus, *Eurymerodesmus* is still unknown from piedmont North Carolina. I have searched for it repeatedly in Duke Forest and neighboring areas at appropriate times of the year without success.

In Florida, *v. varius* inhabits a variety of biotopes. In Gilchrist County I found a sizeable population in and under exposed, rotting oak logs and stumps on sandy substrate. Large populations were also encountered in hardwood litter at Fort Caroline, Duval County, and Marjorie Kinnan Rawlings State Historic Site, Alachua County. The latter site is a mesic hardwood hammock dominated by sweet gum, laurel oak, and cabbage palm without pine.

The Hernando County locality also is a hardwood forest, but it contains more oak trees and is more xeric.

Distribution. — The Atlantic and Gulf Coastal Plains of the southeastern United States, from southeastern North Carolina to Hernando County, Florida, and inland to the Fall Zone Region of Alabama and Georgia as far west as Mississippi (Fig. 54). I investigated many sites in peninsular Florida in January 1988 to determine the southern range limit for the species and family along the Atlantic Coast and did not find it east of the St. John's River. Consequently, Ft. Caroline, less than 10 miles from the ocean, is the only known locality in eastern Florida. On the western side of the peninsula I extended the range southward about 80 miles, from Gainesville to northern Hernando County, but did not encounter the milliped farther south, even in hardwood areas around Brooksville where *Sigmoria (Cheiropus) planca* (Loomis) occurs (Shelley 1984b). These hardwood communities end in Hernando County, and the habitat around Tampa Bay and farther south is unsuitable. Consequently, northern Hernando County seems to be near the actual southern range limit for both *v. varius* and the Eurymerodesmidae along the Atlantic Coast. No records are available from South Carolina, but the milliped should be expected throughout the southeastern Coastal Plain judging by its occurrence in North Carolina and the general uniformity of coastal environments in the Carolinas and Georgia. I doubt if this is an allopatric locality, as occur in *hispidipes* and *serratus*, and the absence of South Carolina records probably reflects the absence of winter collecting. Specimens were examined as follows:

NORTH CAROLINA: *Robeson Co.*, 1.2 mi. SW Proctorville, along SR 2265, 0.4 mi. W jct. NC hwy. 130, M, 17 April 1984, D. Hedgepeth (NCSM); 28M, 20F, 17 April 1985, R. M. Shelley and J. Alderman (NCSM); and 6M, 9F, 4 November 1986, R. M. Shelley (NCSM).

GEORGIA: *Monroe Co.*, 5 mi. N Lizella, 2M, F, 19 February 1983, J. A. Payne (RLH). *Bibb Co.*, Macon, juv. M, date unknown, L. M. Underwood (NMNH). *Talbot Co.*, Geneva, 2F, 24 April 1960. L. Hubricht (RLH). *Baker Co.*, near Newton, Pineland Plantation, 5M, 4F, 30 March 1959, D. B. Jester, H. Wyatt (FSCA). *Worth Co.*, 4 mi. E Sylvester, 6F, 6 juvs., 11 June 1959, N. B. Causey (FSCA). *Seminole Co.*, 4 mi. NW Donaldson, 4M, 3F, 18 March 1961, L. Hubricht (RLH). *Decatur Co.*, near Spring Cr. W of Brinson, 2M, F, 18 March 1961, L. Hubricht (RLH). *Grady Co.*, 3 mi.

W Cairo, 3M, 3F, 26 January 1965, N. B. Causey (FSCA).

FLORIDA: *Duval Co.*, Ft. Carolina, 6M, 7F, 8 November 1985, R. M. Shelley (NCSM). *Alachua Co.*, Gainesville, F, 29 October 1959, W. J. Platt (FSCA); and Marjorie K. Rawlings St. Hist. Site, 31M, 22F, 21 January 1988, R. M. Shelley and G. B. Edwards (NCSM). *Gilchrist Co.*, S. of Trenton, 6 juvs., 2 April 1959, R. E. Woodruff (FSCA); and along FL hwy. 340 at Suwannee R., 19M, 14F, 6 November 1985, R. M. Shelley (NCSM). *Hernando Co.*, 7 mi. NNE Brooksville, along US hwy. 40, 2M, 3F, 22 January 1988, R. M. Shelley (NCSM). *Leon Co.*, Tall Timbers Res. Sta., 34M, 22F, 23 April 1969-24 January 1972, P. Fall, W. W. Baker, and W. H. Whitcomb (FSCA); and Tallahassee, F, 10 November 1958, R. McFarland (FSCA). *Jefferson Co.*, locality and collector unknown, 47M, 31F, 20 November 1968 - 7 February 1969 (FSCA); and Big Bend Hort. Lab near Monticello, 52M, 32F, 2 February 1969 - 12 December 1969, W. H. Whitcomb (FSCA). *Jackson Co.*, Marianna, F, 6 June 1970, D. C. Bennett (FSCA), M, date and collector unknown (MCZ), and juv., 27 October 1941, E. M. Loomis (NMNH); and Florida Caverns St. Pk., 19 juvs., 27 May 1958 - 2 July 1960, N. B. Causey (FSCA). *Okaloosa Co.*, locality unknown, 5M, 10F, 14 March 1961, H. A. Denmark (FSCA). *Escambia Co.*, Pensacola, F, March-April 1986, C. H. Bollman (NMNH), and 3M, 5F, 15 March 1970, C. Seal (FSCA) TYPE LOCALITY; Cantonment, 5M, F, 1 May 1954, N. B. Causey (FSCA); and 5 mi. S Atmore, AL, F, 27 November 1964, E. Harvey (FSCA).

ALABAMA: *Perry Co.*, 6 mi. NW Marion, 3F, 6 January 1954, N. B. Causey (FSCA). *Lee Co.*, Auburn, M, 4F, date unknown, B. B. Warwick (NMNH), 2M, 2F, 1898, F. Farley (NMNH), and M, 6F, 3 juvs., 13 June 1959, N. B. Causey (FSCA). *Houston Co.*, "Brannon Stand" along US hwy. 84, 2M, 3F, 10 juvs., 26 January 1954, N. B. Causey (FSCA). *Mobile Co.*, "Seven Hills," 5M, 2F, 6 April 1958, S. Lazell (FSCA); Bellingrath Gardens, M, 22 January 1965, N. B. Causey (FSCA); and roadside park along US 90 E of Pascagoula, MS, 3F, 21 January 1965 (FSCA).

***Eurymerodesmus varius christianus* Chamberlin,  
new status**

Figs. 54, 64-65, 211

*Eurymerodesmus christianus* Chamberlin, 1946:140, fig. 5.  
Chamberlin and Hoffman, 1958:79. Causey, 1963:77-78.



*Type specimens.* — Male holotype, female allotype, and two male paratypes (NMNH) collected by J. and W. Rapp, 16 February 1946, at Pass Christian, Harrison Co., MS. As stated in the species account, these specimens actually belong to intergrade populations, but since no name is available for the lobed form in eastern Louisiana and this site is only about 35 miles to the east, it is appropriate to conserve *christianus* and assign it to this race.

*Diagnosis.* — A small subspecies; males with projection of mandibular stipes minute, nubbinlike, indistinct; acropodite discontinuous with, and sharply demarcated from prefemur; latter with high, rounded distal lobe, strongly elevated above distal margin (Figs. 64-65).

*Variation.* — In some males, the corner of the division point of the aperture extends downward well into the opening, nearly touching the gonopodal coxae, and in specimens from East Baton Rouge Parish, the outer caudal margin is rimmed and extends into the opening. On the gonopods the prefemoral lobe in some males leans dorsad rather than being aligned with the stem.

*Ecology.* — Specimens from East Baton Rouge Parish were collected in magnolia woods and under dead leaves and grass around a house foundation.

*Distribution.* — Southeastern Louisiana between the Pearl and Mississippi Rivers (Figs. 54, 211). Specimens were examined as follows:

LOUISIANA: *Washington Par.*, Angie, 2M, 2F, 2 May 1958, J. L. Crain (FSCA) and 68M, 79F, 12 December 1958, collector unknown (FSCA); 7 mi. S Angie, 10M, 4F, 16 and 24 November 1958, J. L. Crain (FSCA); and 6 mi. SW Bogalusa, 2F, 21 January 1965, N. B. Causey (FSCA). *St. Tammany Par.*, 5 mi N Hickory, F, 21 February 1965, W. Longest (FSCA); and 1 mi. E Covington, 2 juvs., 2 December 1980, M. R. and J. E. Cooper (NCSM). *Tangipahoa Par.*, 1 mi. N Hammond, F, 23 December 1964, R. E. Randy (FSCA); and 6 mi. E Ponchatula, 24 March 1962, K. A. Arnold (FSCA). *St. Helena Par.*, Grangeville, M, 11 December 1963, S. Geauthreaux (FSCA). *Livingston Par.*, 2.8 mi. W Killian, F, 2 May 1971, D. A. Rossman (FSCA). *East Feliciana Par.*, nr. S gate LA state prison, 3M, 3F, 1970, collector unknown (FSCA). *Ascension Par.*, nr. Prairieville, 6M, 3F, 20 January 1965, W. Longest (FSCA). *East Baton Rouge Par.*, locality unknown, 2M, 5F, 4 November 1959, collector unknown (NMNH) and 3M, 3F, 7 November 1964, collector unknown (FSCA); Baton Rouge, 2M, 3F, November 1969, and M, 2F, 25 October 1964, collectors unknown (FSCA), 2M, F, 11 November

1963, W. J. Harman (FSCA), and M, F, 2 juvs., 9 January 1971, D. A. and C. E. Rossman (FSCA); LSU and environs, 3M, 2 February 1964, and M, F, 9 juvs., 12 December 1964, R. E. Tandy (FSCA); and LSU farm, M, 20 February 1963, B. Hepburn (FSCA).

***Eurymerodesmus varius louisianae* Chamberlin,**  
new status

Figs. 54, 66-71, 211

*Eurymerodesmus louisianae* Chamberlin, 1942a:6, pl. 2, fig. 17.

Chamberlin and Hoffman, 1958:80.

*Eurymerodesmus spectabilis* Causey, 1950a:270, figs. 6-7;

1952b:2. Chamberlin and Hoffman, 1958:81. NEW

SYNONYMY.

*Type specimens.* — Male holotype and one male paratype (NMNH) collected by L. Hubricht, 12 April 1936, 2 mi. S Saline, Natchitoches Par., LA. The original description (Chamberlin 1942a) stated that the type series contained a male and female, labeled allotype in the vial, an example of sex mis-determination.

*Diagnosis.* — A small to moderate-size subspecies; males with projection of mandibular stipes distinct, moderately long, triangular to blunt (Figs. 66-67); acropodite poorly to moderately demarcated from prefemur; latter with variable distal swelling weakly to moderately elevated above distal margin (Figs. 69-71).

*Color in Life.* — Paranota red; metaterga dark brown with red stripes along caudal margins, probably connecting with paranotal markings (Chamberlin 1942a). Causey (1950a) confirmed the striped pattern, reporting orange rather than red and stripes along both margins of the collum. She noted further that the metatergal stripe is interrupted on some caudal segments, that the stripe is replaced by four orange dots in some specimens, and that the orange pigment was so intense in some individuals that they appeared entirely orange from a distance.

*Variation.* — The holotype has an oblong, blunt mandibular process (Fig. 66), but it is triangular (Fig. 67) in the paratype, presumably collected at the same place and time. Both conditions are also displayed by males in Avoyelles and Catahoula parishes. The Arkansas male and those from Rapides and Avoyelles parishes have moderate distal swellings on the gonopod prefemora (Fig. 71), resulting in a slightly discontinuous, moderately demarcated acropodite. The telopodites of individuals from Natchitoches and Rapides parishes curve more dorsad than laterad, best seen *in situ*

(Fig. 68). Thus, they resemble the condition in *amplus*, but they lack continuous hairs on the prefemoral stem. Some males of this race have more prefemoral hairs than do those of the other subspecies, but the hairs are not continuous or regularly spaced. Thus, the main distinctions between *amplus* and *v. louisianae* are the regularity of hairs on the prefemoral stem combined with the *in situ* orientation of the gonopods.

*Ecology.* — According to Causey (1950a), the Arkansas specimens were taken in a climax pine-hardwood area. The label with the type specimens states that they were encountered under logs; that with the Rapides Parish specimens indicates that they were found under cow dung.

*Distribution.* — Known from six scattered localities from southern Arkansas to central Louisiana (Figs. 54, 211). Specimens were examined as follows:

ARKANSAS: *Columbia Co.*, Magnolia, M, F, 24 December 1949, N. B. Causey (ANSP).

LOUISIANA: *Natchitoches Par.*, 2 mi. S Saline (in Bienville Par.), 2M, 12 April 1936, L. Hubricht (NMNH) TYPE LOCALITY. *Vernon Par.*, 2.7 mi. NE Caney, M, 8 April 1967, L. D. Wilson (FSCA). *Avoyelles Par.*, Evergreen, M, 28 October 1965, M. Kordish (FSCA). *Rapides Par.*, Forest Hill, 2M, F, 11 December 1945, R. Wenzel (FMNH). *Catahoula Par.*, 1 mi. WNW Harrisonburg, 2M, F, 25 April 1971, D. A. Rossman (FSCA).

*Remarks.* — Causey (1963) recorded this form from an unspecified locality in Union County, Arkansas. The specimens were supposedly in her collection, but they are not among the material now at the FSCA.

With only six scattered samples from an area that has been reasonably well collected, *v. louisianae* may be a relictual form, declining naturally toward extinction. The most obvious cause would be swamping by *amplus*, which is widespread and abundant in Louisiana west of the Mississippi River. However, much more field work is necessary in this area to search for *v. louisianae* as well as components of the *simplex* group.

Shelley and Whitehead (1986) defined subspecies in *Sigmoria* as reasonably homogeneous taxa that connect with other such taxa through intergrades. Populations had to be continuous for subspecies to be applicable; when there were hiatuses, the species category was employed even if intermediates were known. Populations of *varius* are continuous up to the Mississippi River, then there is a gap of about 40 miles to the closest known site of *v. louisianae*, in

Avoyelles Parish. I therefore debated for some time the status of this race before reasoning that the similarities between the gonopods of *v. louisianae* and those of the other races is so close that specific status based solely on the mandibular projection was unreasonable. This decision should be reviewed by future workers with access to more material and particularly ones who can sample between West Feliciana and Avoyelles parishes, to try to connect *v. louisianae* and *v. christianus*.

Aside from fewer prefemoral hairs, the differences between *v. louisianae* and *amplus* are subtle. They differ in size, with *v. louisianae* being small while *amplus*, though variable, is larger. The apertures of *v. louisianae* and the form of *amplus* in northern Louisiana are closely similar, but there are gonopodal distinctions. Best seen *in situ*, the acropodites bend more strongly from the prefemur and are directed more laterad in *v. louisianae*, whereas in *amplus* they are curved and extend in a dorsal direction thus being more continuous with the axis of the prefemur. Finally, the prefemur of *v. louisianae* often exhibits a slight but distinct distal swelling on the outer surface, whereas there is no trace of this feature in *amplus*. The combination of this swelling and the sparsely hirsute condition resembles that in *v. christianus*. Causey (1963) provides a clue to the status of *v. louisianae* by placing the synonym *spectabilis* under *christianus*, indicating that she too was influenced by the prefemoral similarities, particularly the sparse hairs.

The similarities between *v. louisianae* and *amplus* pose a difficult taxonomic problem. Since some males of the former have more prefemoral hairs than occur on other subspecies, they could be regarded as intergrades between the sparsely and sporadically hirsute stems and those with dense, continuous hairs. Furthermore, the acropodites of some males of *v. louisianae* are more aligned with the prefemur and curve dorsad *in situ* rather than laterad, a condition that could also be interpreted as intermediate between *varius* and *amplus*. Thus, the question arises as to whether *amplus* and *varius* are indeed reproductively isolated, and the argument that they should be combined carries considerable merit. Others analyzing the available material might consider some of my samples of *v. louisianae* to be *amplus*. For clarity, I separate these forms and describe the situation. The complexity in a single species combining the multitude of forms of *varius* and *amplus* is more than I can handle on first revision, and additional material may always clarify the picture. Final resolution is therefore left to future



workers, particularly persons in Louisiana who can meticulously sample its eurymerodesmid fauna.

### **Eurymerodesmus varius intergrades**

Figs. 54, 62-63

I combine under this heading forms with moderate distal prefemoral swellings (Figs. 62-63), intermediate between the strong lobes of *v. christianus* and the slight enlargements of the nominate subspecies. As stated in the species account, the enlargements become more noticeable in Mississippi, and the boundary of the strongly lobed race is sharp, the Pearl River. Thus, I consider all records of *varius* from Mississippi as intergrades.

*Ecology.* — The following habitat notes are on vial labels: under strawberries in strawberry field, and under boards and rocks, Jackson Co.; "waste ground," Lauderdale Co.; and in pitfall traps in cotton field, Oktibbeha Co.

*Distribution.* — Mississippi (Fig. 54). Specimens were examined as follows:

MISSISSIPPI: *Panola Co.*, 13 mi. E Como, 5M, 3F, 25 December 1964, W. Longest (FSCA). *Monroe Co.*, Aberdeen, 3M, 3F, 6 March 1961, R. E. Hutchins (FSCA). *Oktibbeha Co.*, Craig Springs, 10 mi. S Starkville, 18M, 23F, juv., 1 October - 31 December 1979, W. H. Cross (MEM, NCSM). *Newton Co.*, Decatur, many juvs., 5 May 1933, H. Janes (NMNH). *Lauderdale Co.*, Meridian, 1st St. and 53rd Ave., 5M, 6F, 10 December 1961, L. Hubricht (RLH). *Stone Co.*, MS hwy. 15 at Harrison Co. line, 2F, date unknown, N. B. Causey (FSCA). *Jackson Co.*, Pascagoula, 2M, 3F, 12 February 1962, T. Sheldon (FSCA); Spanish Fort, 10M, 4F, 21 January 1965, N. B. Causey (FSCA); 3 mi. N Fontanbleau, 11M, 12F, 1 January 1954, N. B. Causey (FSCA); and Gulf Coast Res. Lab, Ocean Springs, 3M, 7F, 27 November 1964, C. Guise (FSCA). *Harrison Co.*, Biloxi, 20 juvs., 12 July 1927, H.A. Robinson (NMNH). Gulfport, M, 2F, 18 November 1922, E. K. Bynum (NMNH); and Pass Christian, 2M, 2F, 16 February 1945, J. and W. Rapp (NMNH).

*Remarks.* — The type collection of *christianus* contains a gonopod of *angularis* that appears to have been accidentally placed in the wrong vial, probably by Causey when she was examining and comparing eurymerodesmids years ago. A gonopod of the holotype of *wellesleybentoni*, a synonym of *angularis*, is missing, and the extraneous gonopod in the *christianus* vial conforms closely to the remaining one in the *wellesleybentoni* vial.

### **Eurymerodesmus amplus Causey**

Figs. 54, 72-82, 211-212

*Leptodesmus hispidipes*: Brolemann, 1895:67. Chamberlin, 1918:370 (in part).

*Fontaria (Eurymerodesmus) hispidipes*: Brolemann, 1900:129, fig. 32.

*Eurymerodesmus amplus* Causey, 1952b:4, fig. 3. Chamberlin and Hoffman, 1958:78.

*Eurymerodesmus hamatilis* Loomis, 1969:250-251, figs. 11-13.

NEW SYNONYMY.

*Eurymerodesmus hispidipes*: Stewart, 1969:384.

*Type specimens.* — Male holotype and female allotype (AMNH) collected by W. J. Harmon in November 1951 at Ruston, Lincoln Par., LA.

*Diagnosis.* — A moderate-size species; males characterized by long mandibular projections; sides of aperture divided, with variably closed to partly open pouch; telopodite long; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners extending into distinct ridge of variable length and configuration, sublinear or angling toward corner, with or without terminal papilla in more angular forms; receptacle moderate-size, sides curving partly around operculum.

*Color in Life.* — Paranota red; metaterga dark speckled olive with red stripes along caudal margins connecting paranotal spots, stripes partly obliterated by intrusions of base color; collum with red stripe along anterior margin.

*Holotype.* — Body highly fragmented, length unmeasurable, maximum width 4.2 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 3.0 mm, interantennal isthmus 0.7 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres 2>3>4>6>5>1>7. Genae with faint central impressions. Facial setae as follows: epicranial and genal absent, subantennal 1-1, frontal 1-1, clypeal about 16-16, labral about 22-22. Process of mandibular stipes moderately long, broadly rounded apically, curving slightly inward at midlength (Fig. 72).

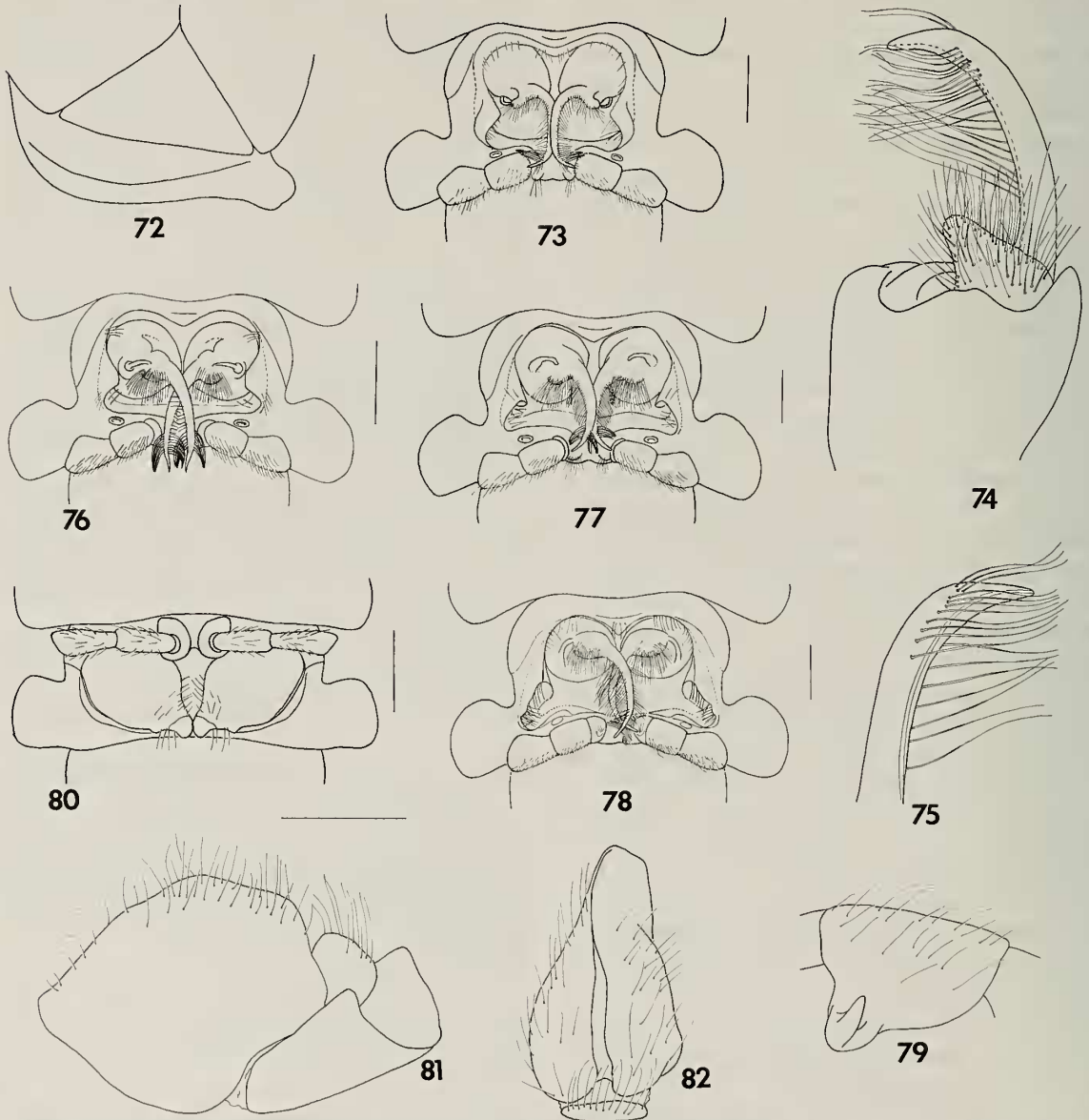
Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 9, blunt on 10-12, becoming progressively more acute caudally.

5th and 6th sterna with widely separated knobs between leg pairs. Postgonopodal sterna with narrowly segregated, elevated patches between 9th legs; remaining sterna becoming progressively flatter and less hirsute caudally. 2nd coxa with large, subconical anterior, and smaller rounded posterior lobes. Prefemora with broad lobes on outer surfaces of legs through segment 11.

Gonopodal aperture (Fig. 73, not this specimen) broadly ovoid, with closed, caudolateral pouches and moderate anterior indenta-

tion, 1.6 mm wide and 1.0 mm long at maxima, outline of entire apparatus irregularly hexagonal; anterior indentation short, apically rounded; sides divided, curving broadly mediad, leaning over opening, elevating gradually to division point near midlength, inner lateral margin curving dorsolaterad then blending smoothly into inner caudal margin, outer lateral margin leaning over opening, angling moderately laterad then curling mediad to metazonal surface at caudolateral corner, forming closed pouch with inner margin, rims slightly irregular; inner caudolateral corner smoothly curved but hidden by overhanging outer lateral margin; outer caudolateral corner moderately sharp, forming approximately a 60° angle; inner caudal margin extending linearly across midline,

not parallel with outer caudal margin; latter curving along anterior surface of coxal condyles, extending caudad in midline; margins irregularly hirsute, with long hairs arising sporadically from anterior rim and overhanging opening, particularly along indentation and anterolateral corners, with additional short hairs arising from outer surface of outer lateral margin and moderate tufts from pouches. Gonopods *in situ* (Fig. 73, not this specimen) with telopodites lying partly over and under one another in midline of aperture, diverging at level of caudal margins, curving gently subdorsad and terminating over 9th coxae. Gonopod structure as follows (Figs. 74-75): Telopodite terminating well before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite



Figs. 72-82. *Eurymerodesmus amplus*. 72, projection of right mandible of holotype, lateral view. 73, aperture and gonopods *in situ* of topotype, ventral view. 74, left gonopod of holotype, lateral view. 75, telopodite of the same, medial view. 76-78, aperture and gonopods *in situ* of males from Evangeline and Calcasieu pars., LA, and Angelina Co., TX, respectively, ventral views. 79, prefemur of left 7th leg of male from Angelina Co., anterior view. 80, cyphopods *in situ* of female from Vernon Par., LA, ventral view. 81, left cyphopod of allotype, ventral view. 82, the same, medial view. Scale lines for figs. 73, 76-78, and 80 = 1.00 mm. Line for other figs. = 0.30 mm for 72 and 79, 0.40 mm for 74 and 81-82, and 0.50 mm for 75.



length, stem leaning over coxa for most of length, more so distad, sides parallel throughout, with two rows of continuous, regularly spaced hairs along inner margin, angling slightly outward distad, and distomedial tuft of about 10 hairs. Acropodite short and broadly terminal, only about 1/8 of telopodite length, continuing curvature of prefemur and directed dorsolaterad, smoothly continuous with, and poorly demarcated from prefemur, sides narrowing continuously to acuminate tip.

*Allotype*. — Length 30.7 mm, maximum width 4.2 mm, W/L ratio 13.7%. Agreeing closely with holotype in somatic features, with following exceptions: Process of mandibular stipes relatively large, extending distinctly from base, broadly triangular. Sterna with variably broad impressions in midline, with sparse hair tufts subtending coxae except on segments 17-18.

Cyphopodal aperture broadly rectangular, sides strongly elevated above metazonal surface. Cyphopods *in situ* with corners of valves protruding through opening, valves oriented transversely. Valves (Figs. 81-82) large, subequal, ventral margin elevated into rim, angling slightly distad and slightly longer at corner, medial margin moderately hirsute. Receptacle moderately large, glabrous, located laterad at bases of valves, sides curving partly around operculum. Latter small, hidden under free (anterior) side of valves.

*Variation*. — The colors reported above were of the specimens I collected in Harris County, Texas. According to Causey (1952b), the paranota of the types were reddish orange; she provided no additional color details. The label accompanying the specimens from Sulphur, Calcasieu Parish, Louisiana, states "orange," presumably referring to the paranota, so the color of this species may vary.

*Eurymerodesmus amplus* is difficult to comprehend on its own merits, not to mention the close similarities with *v. louisianae*. The gonopods exhibit little intraspecific variation, but there are three main aperture variants that tend to occupy different sectors of the range thus suggesting that subspecies may be warranted. However, there are enough instances where one variant also occurs in another sector or there are additional sympatric forms, that this possibility is obviated. Moreover, the anatomical diversity is greater in Texas, and one or more heterogeneous races there would conflict with comparatively homogeneous ones in Louisiana. Finally, female variation is not parallel and would therefore counter subspecies based on males. By not showing comparable differences at fairly sharp male boundaries, females also contraindicate specific statuses for the principle male variants. Females show a general clinal trend toward a longer and more angular valvular ridge in a southerly direction. Individuals from northern areas like Lincoln and Natchitoches Parishes have distinct, but only slightly elevated, ridges that are either linear or angle slightly laterad toward the distal corner. In southern Louisiana the rim is distinctly longer at this corner and therefore obviously slanted in this direction. This

variant extends into western Louisiana and eastern Texas, and in many individuals the medial corner is additionally prolonged into a papilla or short digitiform projection (Fig. 80). As with males, females are more variable in Texas than in Louisiana, and the overall picture in both states is extremely complex when one considers both sexes. Conclusions based on one sex are contradicted by the other, and in general female variation traverses the boundaries between male forms. I therefore regard *amplus* as a single highly variable species with three principle male morphs, which are characterized in the ensuing paragraphs along with lesser forms in Texas.

The first variant is represented by the holotype and occurs in northern Louisiana (Lincoln, Natchitoches, Desoto, Bienville, Red River, Sabine, and eastern Vernon parishes), extends across the Sabine River into Harrison County, Texas, and occurs sporadically to the west in Texas (Wood, Anderson, Tyler, and to a lesser extent Nacogdoches counties). In this form (Fig. 73), the aperture sides are moderately high and lean well over the opening at division point; the inner lateral margin extends downward or dorsad into the opening, and the outer lateral margin flares moderately laterad, all combining to form a distinct closed pouch. In addition to the rim, females in this area display a variable indentation on the medial valvular surface that is greater in individuals from the northern periphery of the third male variant, thus constituting another trait traversing a boundary between male forms.

The second male variant (Fig. 76) occurs to the south in Evangeline, Jefferson Davis, and Iberia parishes Louisiana. Here the sides of the aperture are more strongly elevated and upright from the anterolateral corner to division point. The outer lateral margin does not angle as strongly laterad and in some specimens is nearly colinear with the anterior part of the sides. The inner lateral margin is directed downward, and the net effect is a shallower pouch that is virtually absent from a few males. A similar form occurs in Montgomery County, Texas, and one in Nacogdoches County is intermediate between this and the first morph.

The third variant occurs in western Louisiana (western Vernon, Beauregard, Calcasieu, and Cameron parishes) and eastern Texas (Shelby, Jasper, Rusk, Smith, Polk, Houston, Grimes, Chambers, Galveston, and Harris counties) where it intermixes with the other two forms. Here the sides rise gradually to division point, which leans strongly medially over the opening (Fig. 77). The inner lateral

margin extends slightly inward into the opening before curving broadly dorsad, and the outer lateral margin angles moderately laterad, forming a deep, moderately open pouch. This morph intermixes in eastern Texas with the second variant and with that named *hamatilis* by Loomis (1969) (Fig. 78), in which the pouch is even deeper and more open because the outer lateral margin flares strongly laterad and the inner margin extends submediad into the opening before curving dorsad. Thus, although the sides do not lean strongly over the opening, the pouch is still broad and deep because of the initial invagination of the inner lateral margin. As noted by Loomis (1969), this variant also possesses a sclerotized hook on the anterior surfaces of the prefemora on the 7th and 9th legs (Fig. 79). This type of aperture is known from three widely separated localities in Angelina, Panola, and Mason counties, the latter sites respectively about 66 miles north and 280 miles west of the first. The Mason County record represents an apparently allopatric population in the midst of *melacis*, some 200 miles west of the closest known site of either *amplus*, the *varius* group, or the *Kewanius* lineage. In the area of eastern Texas occupied by the third variant, the valvular rim in females slopes strongly mediad, usually culminating in a variably papillate to digitiform projection on the distal corners (Fig. 80), the projection tending to be longer and more digitiform to the south. However, some females in this area lack papillae and exhibit slanted rims. The form named *hamatilis* is recognizably different, but the situation with females and sympatry with other males indicates that it is merely one variant of a highly variable species. Consequently, *hamatilis* is a junior synonym of *amplus*.

*Ecology.* — The male I collected in July 1980 in Harrison County, Texas, the wrong season for eurymerodesmids, consisted of loose exoskeletal rings without appendages and was identified from the aperture configuration. The segments were found under leaf litter beside a building at Caddo Lake State Park. The specimens from Harris County were discovered under logs beside a trail in a predominantly pine habitat at Memorial Park, Houston. Habitat notations on other vial labels are as follows: under logs and boards in a bottomland meadow adjacent to a pine-hardwood forest (Red River Par., LA), in a rotting shed (Sabine Par., LA), at a plant nursery (Jefferson Davis Par., LA), under sawdust (Vernon Par., LA), under a log (Nacogdoches Co., TX), in a greenhouse (Smith Co., TX), and on a prairie (Chambers Co., TX).

The sample from near Steinhagen Lake, Tyler County, Texas, was discovered by ultraviolet light at night, apparently fluorescing.

*Distribution.* — Louisiana from the Mississippi River and the Atchafalaya Bayou to the middle Trinity and lower Brazos Rivers in eastern Texas, with an allopatric population 200 miles to the west on the eastern periphery of the Edwards Plateau in Mason County (Figs. 54, 211-212). Specimens were examined as follows:

LOUISIANA: *Lincoln Par.*, Ruston, M, F, November 1951, W. J. Harmon (AMNH) and 4M, juv., 2 January 1953, F. L. Afeman (FSCA) TYPE LOCALITY. *Bienville Par.*, Castor, 2M, 21 November 1954, J. E. Sublette (FSCA). *Natchitoches Par.*, Creston, 14M, 8F, 27 February-5 May 1915, K. P. Schmidt (MCZ); Grand Ecore, M, 26 October 1934, J. E. Sublette (FSCA); Natchitoches, M, 13 November 1953, B. Stanberry (FSCA) and M, 25 February 1954, J. E. Sublette (FSCA); and Kisatchie, M, F, 30 October 1954, W. J. Harmon (FSCA). *Avoyelles Par.*, Evergreen, F, 23 December 1965, M. Kordisch (FSCA). *Red River Par.*, 3.7 mi. NW Coushatta, 4M, 3F, 10 April 1971, P. J. Kinnick (FSCA); and Coushatta, M, 28 November 1953, Bamburg (FSCA). *Desoto Par.*, along US hwy. 171, 2.5 mi. N Mansfield, 4M, 13 March 1966, R. E. Tandy (FSCA). *Sabine Par.*, Hodges Garden, along US hwy. 171 N of Sandel, 2M, 7F, juv., 26 March 1965, R. E. Tandy, G. E. Gates (FSCA). *Vernon Par.*, unknown locality, F, 17 June 1956, J. E. Sublett (FSCA); LA hwy. 111, 1.9 mi. N. jct. LA hwy. 464, F, 19 February 1966, R. E. Tandy (FSCA); 2.4 mi. ENE Pitkin, 3M, 3F, 20 February 1966, R. E. Tandy (FSCA); near Sabine R. on LA hwy. 8, 4M, 2F, 25 March 1965, R. E. Tandy, G. E. Gates (FSCA); and along LA hwy. 464, 11.5 mi. SSW Caney, M, 19 February 1966, R. E. Tandy (FSCA). *Allen Par.*, West Bay Game Area, F, 2 October 1965, L. D. Wilson (FSCA). *Beauregard Par.*, US hwy. 190 at Sabine R., F, 30 April 1966, R. E. Tandy (FSCA); and DeRidder, 8M, 6F, 20 March, 17 October, and 9 December 1969, H. Rhame (FSCA); and 5 mi. S DeRidder, 6M, 3F, 22 juvs., 10 December 1969, H. Rhame (FSCA). *Evangeline Par.*, Lake Chicot, F, 20 March 1965, M. Kordisch (FSCA); 2.5 mi. S Chicot St. Pk., M, 30 January 1968, E. D. Kaiser (FSCA); and Boggs Bayou, 2.7 mi. W jct. LA hways. 106 and 13, M, F, 9 January 1966, R. E. Tandy (FSCA). *Iberia Par.*, Avery Island, M, F, juv., 7 April 1974, N. B. Causey (FSCA). *Acadia Par.*, I-10 at Mermentau R., 2F, 26 September 1965, R. E. Tandy (FSCA).



*Jefferson Davis Par.*, Elton, 14M, 11F, 29 November 1964 and 1 March 1965, C. Steal (FSCA). *Calcasieu Par.*, Lake Charles, M, juv., 15 April 1965, and 4M, 4F, 28 April 1967, M. Kordish (FSCA); Sulphur, 4M, 4F, 22 February 1965, collector unknown (FSCA); and 10 mi. W Lake Charles, M, F, 18 November 1964, M. Kordish (FSCA). *Cameron Par.*, 5 mi. W Holly Beach, M, 29 April 1962, K. Arnold (FSCA).

TEXAS: *Harrison Co.*, nr. Waskom, 2F, 25 March 1962, N. B. Causey (FSCA); and Caddo Lake St. Pk., M (exoskeletal fragments), 11 July 1980, R. M. Shelley (NCSM). *Panola Co.*, Carthage, 3M, 3F, 10 March and 24 November 1962, L. P. Hull (FSCA). *Shelby Co.*, Paxton, 13M, 8F, date and collector unknown (FSCA). *Wood Co.*, Alba, 5M, 3F, 2 juvs., 7 February 1932, collector unknown (NMNH). *Smith Co.*, Tyler, 2M, 28 December 1964, T. C. Stewart (FSCA). *Rusk Co.*, along US hwy 259, 5 mi. N Mt. Enterprise, M, 19 November 1967, T. C. Stewart (SFAU); along FM 836, 3 mi. N New Salem, 4M, 3F, 17 November 1967, T. C. Stewart (FSCA); along FM 834, 3 mi. S New Salem, F, 3 juvs., 17 November 1967, T. C. Stewart (SFAU); and Lufkin, juv. M, 22 May 1940, S. and D. Mulaik (NMNH). *Anderson Co.*, Palestine, 3M, 3F, 3 juvs., 26 January 1962, J. O'Keefe (FSCA). *Houston Co.*, Crockett, 6M, 3F, 4 December 1961, L. Heard (FSCA). *Nacogdoches Co.*, Nacogdoches, 10M, 6F, November 1931, collector unknown (NMNH) and M, 11 October 1966, T. C. Stewart (SFAU); and Stephen F. Austin Forest, 2M, 16 March 1968, J. Reddell (FSCA). *Angelina Co.*, 8 mi. N Zavalla, near Sam Rayburn Res., 4M, F, 4 juvs., 23 April 1967, J. C. Loomis (NMNH, FSCA); and county airport, F, 13 October 1966, J. A. Kelgey (SFAU). *Jasper Co.*, Jasper, 26M, 32F, juv., 15 January-25 March 1962, J. DuRard (FSCA). *Tyler Co.*, Woodville, 12M, 14F, 8 juvs., 22 February 1962, R. Timbrook (FSCA); and along US hwy. 190 at Steinhagen L., 25M, 4F, 20 October 1985, J. C. and J. E. Cokendolpher (NCSM). *Polk Co.*, Dallardsville, 2M, juv., 24 February 1962, J. P. Kennedy (FSCA). *Grimes Co.*, Navasota, 7, January 1931, collector unknown (NMNH) and M, F, 5 juvs., 2 December 1961, W. Watkins (FSCA). *Montgomery Co.*, Conroe, 5M, 2 juvs., 10 March 1963, B. Ray (FSCA). *Harris Co.*, Houston, F, 20 December 1930, collector unknown (NMNH) and Memorial Pk., M, 2F, 18 February 1986, R. M. Shelley (NCSM). *Chambers Co.*, Smith Point, 4M, 2F, 3 November 1918, Hansen and Barber (NMNH). *Galveston Co.*, La Marque, 4M, 9F, 7

juvs., date unknown, W. A. Benton (FSCA); and Galveston Island, 2M, F, 1870, W. Julich (MCZ). *Mason Co.*, 1 mi. NE Mason, 3M, 8 November 1964, J. Reddell (FSCA).

*Remarks.* — The specimens from an unspecified site in Louisiana and reported by Brolemann (1895) as *Leptodesmus hispidipes* are *amplus*. This sample consists of 11 males and 2 females and is housed at the MNHP. Brolemann (1900) did not mention a locality, but I believe he was referring to this sample when he proposed *Fontaria (Eurymerodesmus) hispidipes*. The specimens from Creston, Natchitoches Parish, Louisiana, which Chamberlin (1918) also recorded as *Leptodesmus hispidipes*, are mostly *amplus*, though they also contain a male of *birdi*. An *amplus* male from this site measured 29.1 mm long, 4.3 mm wide, W/L ratio 14.8%. Finally, the records of *E. hispidipes* by Stewart (1969) from Angelina, Nacogdoches, Rusk and Smith, counties, Texas, also refer to *amplus*, and since his records from Sabine, Shelby, and Upshur counties lie within the range, they are shown as literature records of *amplus* in figures 54 and 212.

#### *Eurymerodesmus newtonus* Chamberlin

Figs. 54, 83-88, 211

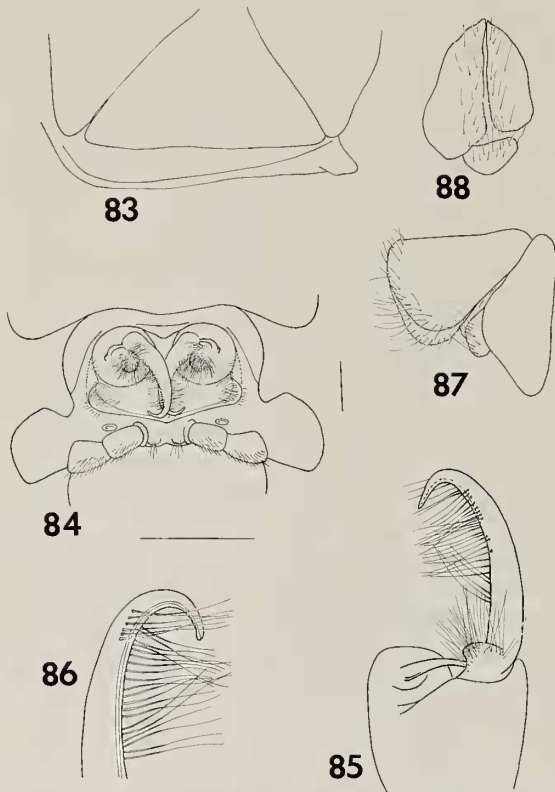
*Eurymerodesmus newtonus* Chamberlin, 1942a:5, pl. 2, fig. 14. Chamberlin and Hoffman, 1958:80.

*Eurymerodesmus bentonus* Causey, 1950a:268-270, fig. 5. Chamberlin and Hoffman, 1958:78. NEW SYNONYMY.

*Type specimens.* — Male holotype and two female paratypes (NMNH) collected by L. Hubricht, 29 April 1936, in the Boston Mountains, 1.2 mi. S Jasper, Newton Co., AR. The head and pregonopodal segments of the holotype are missing, and the male description is therefore based on the specimen from Monte Ne, Benton County, Arkansas, whose gonopods and aperture are virtually identical.

*Diagnosis.* — A moderate-size species; males characterized by moderate-size mandibular projection; sides of aperture divided, with moderately open caudolateral pouches; telopodite long; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, uncinat; prefemur with many hairs arranged continuously along inner surface; cyphopod valves of females not modified, without projections; receptacle moderate-size, sides curving partly around operculum.

*Color in Life.* — Paranota orange; metaterga dark olive with orange stripes along caudal margins connecting paranotal markings; collum with orange stripes along both anterior and posterior borders



Figs. 83-88. *Eurymerodesmus newtonus*. 83, projection of right mandible of male from Benton Co., AR, lateral view. 84, aperture and gonopods *in situ* of male from Washington Co., AR, ventral view. 85, left gonopod of holotype, lateral view. 86, telopodite of left gonopod of male from Benton Co., AR, medial view. 87, left cyphopod of female paratype, caudal view. 88, the same, medial view. Scale line for fig. 84 = 1.00 mm. Line for other figs. = 0.35 mm for 85, 0.40 mm for 83 and 87-88, and 0.50 mm for 86.

(Causey 1950a). Chamberlin (1942a) reported preserved coloration and noted stripes.

*Male from Monte Ne, Benton Co., AR.* Body highly fragmented, length unmeasurable, maximum width 4.8 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.7 mm, interantennal isthmus 0.9 mm. Antennae reaching back to caudal end of 2nd tergite; antennomeres becoming progressively more hirsute distad, relative lengths  $2 > 3 > 5 > 4 > 6 > 1 > 7$ . Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 9-9, labral about 14-14. Projection of mandibular stipes moderately long, apically narrowly rounded (Fig. 83).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum basally, flattened distad; posterior corners rounded through segment 6, blunt on 7-12, becoming progressively more acute posteriorly.

5th sternum with minute lobes between 4th legs and broader elevated areas between 5th legs; 6th sternum with short, para-

median knobs between both leg pairs. Postgonopodal sterna with minute, widely segregated lobes between 9th legs; remaining sterna generally flat and plate-like, with variable transverse impressions originating between leg pairs and moderate hair patches subtending coxae. 2nd legs absent, coxal configuration unknown. Prefemoral lobes broadly rounded, extending through segment 11.

Gonopodal aperture (Fig. 84, not this specimen) ovoid, with partly open caudolateral pouches, slightly indented anteriorly at midline, 1.3 mm wide and 0.4 mm long at maxima, outline of apparatus irregularly hexagonal; anterior indentation short, broad, apically rounded; sides curving slightly mediad and leaning slightly over opening, rising slowly and continuously to division point distal to midlength, inner lateral margin very short, curving immediately into inner caudal margin, outer lateral margin flaring slightly sublateral, not leaning over opening, curving and dropping rapidly to metazonal surface just before caudolateral corner, forming moderate, open pouch with inner margin, rims slightly emarginate; inner caudolateral corner indistinct, smoothly curved continuation of inner lateral margin; outer caudolateral corner broadly curved; inner caudal margin angling caudad, outer third slightly elevated; outer caudal margin angling slightly caudad, more so in midline; anterior margin glabrous, sides with scattered hairs arising from rims beginning along elevation before division point, with short marginal hairs at caudolateral corners and slight tufts from within pouches. Gonopods *in situ* (Fig. 84, not this specimen) with telopodites angling across midline and crossing opposite member, extending to caudal margin then curving laterad, lying nearly completely over and under each other, tips directed dorsolateral. Gonopod structure as follows (Figs. 85-86): Telopodite terminating just before level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, stem curving gently and evenly dorsad for most of length, more so distad, expanding slightly near midlength, narrowing distad, with two rows of continuous, regularly spaced hairs along inner margin and distomedial tuft of about 6 hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, uncinately, curving strongly dorsolateral, poorly demarcated from, and smoothly continuous with, prefemur, narrowing smoothly and continuously to subacuminate tip.

*Female paratype.* — Length 27.0 mm, maximum width 4.2 mm, W/L ratio 15.6%. Agreeing essentially with holotype in somatic features, with following exceptions: Mandibular stipes with short, rounded projection. Sterna flat, with only a few sparse hairs on anterior segments, glabrous thereafter.

Cyphopodal aperture elliptical, caudal margin indented slightly mediad, sides slightly elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely in aperture, central groove visible in opening. Valves (Figs. 87-88) moderately large, unequal, anterior one slightly larger, without lobes or projections, moderately hirsute distad. Receptacle oriented dorsoventrad at bases of valves, forming right angle with latter, curving partly around base of operculum, glabrous. Operculum relatively large, located under valves, partly shielded on anterior and posterior sides by receptacle.

*Variation.* — The holotype gonopods lack the characteristic distomedial tuft of prefemoral hairs that is present on other males. The male from Washington County exhibits a slight distal swelling on the outer prefemoral margin.

*Distribution.* — Known definitely from only three counties in the northwest corner of Arkansas (Figs. 54, 211). Specimens were examined as follows:



ARKANSAS: *Newton Co.*, Boston Mts., 1.2 mi. S Jasper, M, F, 29 April 1936, L. Hubricht (NMNH) TYPE LOCALITY. *Benton Co.*, Monte

*Ecology.* — The material from Benton County reported by Causey (1950a) was collected in predominantly oak woods at the base of a north-facing slope.

Ne, M, 2F, 19 November 1949, N. B. Causey (ANSP, FSCA). *Washington Co.*, Cove Creek Valley, M, Spring 1956, M. Hite (FSCAQ).

*Remarks.* — According to Chamberlin (1942a), the type series of *newtonus* contained the male holotype and three females, two of which are lost.

Causey (1950a) reported collecting numerous specimens of *newtonus* along with *birdi* at Blue Springs, Carroll County, Arkansas. This material also is lost, but the site is within the area circumscribed by the three known counties and thus is plausible for the species. It is shown as a literature record in figures 54, 211.

One of the specimens Causey (1950a) reported from Benton County is an "intersex," labeled a "hermaphrodite" in the vial, with typical cyphopods, gonopods, and genital apertures at the normal locations. The specimen is present in the FSCA and is a functional female with eggs and the female paranota, sterna, and legs. I interpret the gonopods as a developmental accident reflecting the ability of appendages on anterior segments in both sexes to become either legs or gonopods depending on genetic signals. I (1977) summarized examples of this phenomenon in the Xystodesmidae, and it is also exhibited by an accessory gonopod on a male of *b. birdi*. Such accidents are rare in females, and it is noteworthy that the gonopods are at the normal location, the anterior position of segment 7.

### **Eurymerodesmus oliphantus** Chamberlin

Figs. 54, 89-95, 211

*Eurymerodesmus oliphantus* Chamberlin, 1942a:6, pl. 2, fig. 15.

Chamberlin and Hoffman, 1958:80.

*Eurymerodesmus hispidipes*: Causey, 1950a:267-268, figs. 1-4; 1952b, fig. 2. Chamberlin and Hoffman, 1958:191 (in part).

*Type specimens.* — Male holotype and female allotype (NMNH) collected by L. Hubricht, 10 April 1936, 15 mi. SW Oliphant, Jackson Co., AR.

*Diagnosis.* — A small to moderate-size species; males characterized by long mandibular projection; sides of aperture divided, with widely open caudolateral pouches; telopodite long; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur; latter

with many hairs arranged continuously along inner margin; cyphopod valves of females not modified, without projections; receptacle moderate-size, sides curving partly around operculum.

*Color in Life.* — Paranota red; metaterga black with broad, red stripes along caudal margins connecting paranotal markings; collum with red stripes along both anterior and posterior borders (Fig. 89). Chamberlin (1942a) and Causey (1950a) also noted the striped pattern in preserved specimens.

*Holotype.* — Body highly fragmented, length unmeasurable, maximum width 3.8 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.6 mm, interantennal isthmus 0.9 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres  $2 > 3 > 4 = 5 = 6 > 1 > 7$ . Genae without impressions. Facial setae with only clypeal about 8-8, and labral, about 12-12, series. Process of mandibular stipes long, bowed inward, narrowly rounded apically (Fig. 90).

Collum extending slightly below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-10, becoming progressively more acute caudally.

5th sternum with dense hirsute patches adjacent to leg coxae, not elevated; 6th sternum with low, elevated, areas adjacent to leg coxae. Postgonopodal sterna with deep central impression and low, elevated, hirsute areas between 9th legs; remaining sterna generally flat and unmodified, with hair patches adjacent to leg coxae, becoming progressively sparser caudally. 2nd coxa with broadly rounded, subequal anterior and posterior lobes. Prefemoral lobes extending through segment 10.

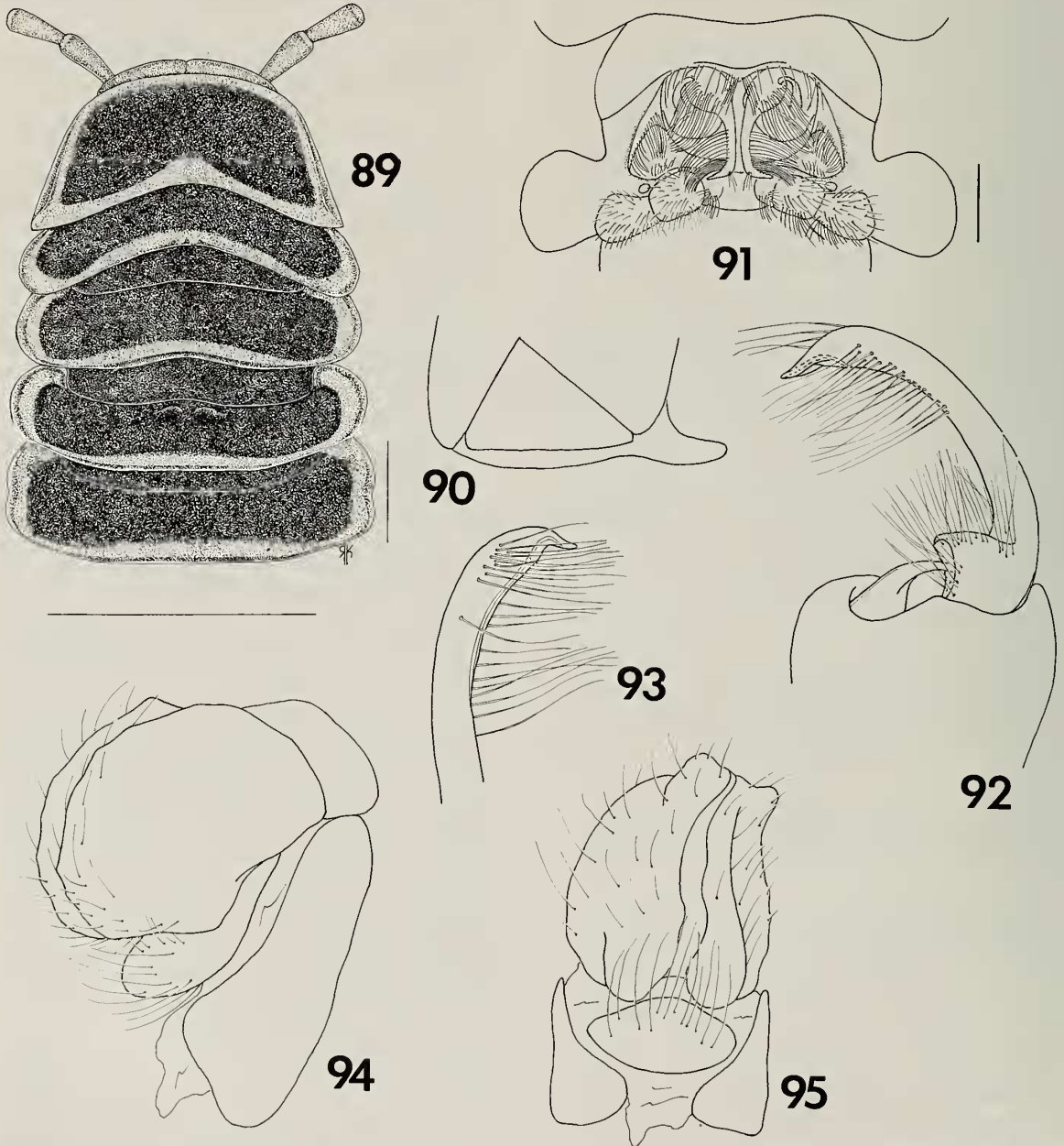
Gonopodal aperture (Fig. 91, not this specimen) ovoid, with open, caudolateral pouches and short, broad anterior indentation, 2.3 mm wide and 0.9 mm long at maxima, outline of apparatus trapezoidal; anterior indentation short, broad; sides curving medially to division point, upright, not leaning over opening, rising progressively to division point at midlength, inner lateral margin continuing curved contours, extending inward, dropping abruptly, and curving smoothly into inner caudal margin, outer lateral margin well separated from inner, flaring strongly and obliquely caudolaterad, lowering progressively to metazonal surface at caudolateral corner, forming broad, deep, open pouch with inner margin, rims of anterolateral margins smooth, those of inner and outer margins slightly irregular; inner caudolateral corners indistinct, broadly rounded; outer caudolateral corners broadly triangular, about 45°; inner caudal margin curving slightly, dropping rapidly to metazonal surface, and extending sublinearly across midline; outer caudal margin curving slightly along anterior surfaces of coxal condyles and continuing as faint line across midline; margins densely and irregularly hirsute, with long hairs arising sporadically from anterior and lateral rims, particularly along anterior indentation and from outer surface of outer lateral margin, and overhanging opening, also with dense tufts of short hairs arising from within pouches, caudal margins glabrous. Gonopods *in situ* (Fig. 91, not this specimen) with telopodites abutting or lying parallel to each other in midline, curving laterad over caudal margins and terminating over 9th coxal condyles, tips directed dorsolaterad. Gonopod structure as follows (Figs. 92-93):

Telopodite terminating well before level of distal extremities of hairs. Prefemur long, about  $7/8$  of telopodite length, leaning over coxa, narrowing slightly to around midlength then expanding, widest at distal extremity, with numerous long hairs arranged continuously in two rows along inner margin and distomedial tuft of about 10 hairs. Acropodite short and broadly terminal, about  $1/8$  of telopodite length, angling dorsolaterad, poorly demarcated from, and smoothly continuous with, prefemur, narrowing rapidly near midlength to acuminate, slightly bisinuate tip.

*Allotype*. — Length 28.4 mm, maximum width 3.8 mm, W/L ratio 13.4%. Agreeing closely with holotype in somatic features,

with following exceptions: Mandibular stipes with short, broadly rounded projection. Sterna flat, nearly glabrous, with at most only an occasional scattered hair.

Cyphopodal aperture subrectangular, sides elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely in aperture, distal surface of anterior valve visible in opening. Valves (Figs. 94-95) relatively large, unequal, anterior valve larger, extending slightly above and overlying caudal valve, moderately hirsute. Receptacle located laterad at bases of valves, relatively narrow, sides curving partly around operculum. Latter large, located under free, dorsomedial side of valves.



Figs. 89-95. *Eurymerodesmus oliphantus*. 89, segments 1-5 of male from Jackson Co., IL, dorsal view. 90, right mandibular process of holotype, lateral view. 91, aperture and gonopods *in situ* of male from Jackson Co., IL, ventral view. 92, left gonopod of holotype, lateral view. 93, telopodite of the same, medial view. 94, left cyphopod of allotype, caudal view. 95, the same, medial view. Scale lines for figs. 89 and 91 = 1.00 mm. Line for other figs. = 0.60 mm for 90 and 92, 1.00 mm for 93-95.



*Variation.* — Measurements of a male from White County, Arkansas, adjacent to Jackson County, are length 23.7 mm, maximum width 3.7 mm, W/L ratio 15.6%.

The most notable variation is the marked reduction in hirsuteness in the southernmost males from Jackson and White counties, Arkansas. All other specimens are extremely hairy, particularly inside the pouches and along the rim and outer surfaces of the outer lateral margins; hence one such male was used to depict the aperture configuration and the *in situ* gonopod arrangement (Fig. 91) rather than the holotype.

The aperture configurations are very similar throughout the range. In males from White County, Arkansas, and Phelps, Pulaski, and St. Louis counties, Missouri, the flare extends more obliquely laterad and tends to lean over the pouch, thus forming a cavity beneath the outer lateral margin from which more hairs arise. The angle of slope of the inner caudal margin can vary from gradual as in the holotype to steep as in males from Pope County, Illinois. The distance between the inner and outer lateral margins, or the rate at which they diverge, also varies, and males in which this distance is greater possess a cavity with hairs beneath the division point.

*In situ* the telopodites may be parallel (Fig. 91) or they may cross each other basally in the midline of the aperture (at the bases of the prefemora) and again distad at the bases of the acropodites above the sternum between the 9th legs. In northern males the acropodite is not apically bisinuate.

The female from St. Louis County, Missouri, the only adult female collected aside from the allotype, agrees with the latter in that the anterior valve is larger than the caudal one.

*Ecology.* — According to vial labels, the males from Pope County, Illinois, were encountered under rocks. I discovered that from Jackson County, Illinois, deeply buried in a rotting oak stump in the Shawnee National Forest.

*Distribution.* — The eastern Ozark Plateau of Arkansas and Missouri and the western Interior Low Plateaus of southern Illinois (Figs. 54, 211). The available samples come from four areas, and field work is needed in the lacunae to determine if they connect. Specimens were examined as follows:

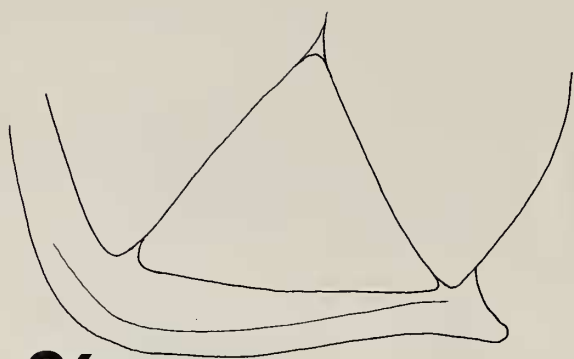
ILLINOIS: *Jackson Co.*, 1.5 mi. W Pomona, along rd. to Pomona Nat. Bridge, M, 15 April 1984, R. M. Shelley (NCSM). *Johnson Co.*, Ferne Clyffe St. Pk., 2M, 27 October 1967, J. A. Beatty (WAS).

*Johnson/Pope cos.*, 3 mi. E Ozark, M, 11 March 1950, P. W. Smith (FSCA). *Pope Co.*, Dixon Springs, 2M, 3 April 1948, Smith, Burks, and Stannard (FSCA, ILNHS).

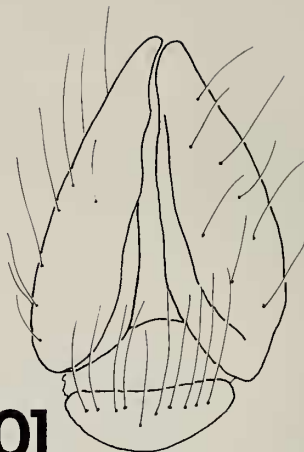
MISSOURI: *St. Louis Co.*, Ranken, exact location unknown, M, F, 2 April 1933 and 17 March 1935, E. P. Meiners (UMO). *Phelps Co.*, 3 mi. NE Rolla, M, 17 April 1965, G. L. Rotramel (ILNHS); and 4 mi. S Jerome, Gable Springs Cv., M, 4 April 1979, J. E. Gardner (NCSM). *Pulaski Co.*, 8 mi. WSW Edgar Springs, Ryden Cv., M, 3 March 1979, J. E. Gardner (NCSM).

ARKANSAS: *Independence Co.*, 1.3 mi. W Cushman, 2M, 2 juv. F, 5 March 1973, R. M. Blaney (FSCA). *Jackson Co.*, 1.5 mi. SW Oliphant, M, F, 10 April 1936, L. Hubricht (NMNH) TYPE LOCALITY. *White Co.*, Russell, M, 25 December 1952, C. Pennington (FSCA).

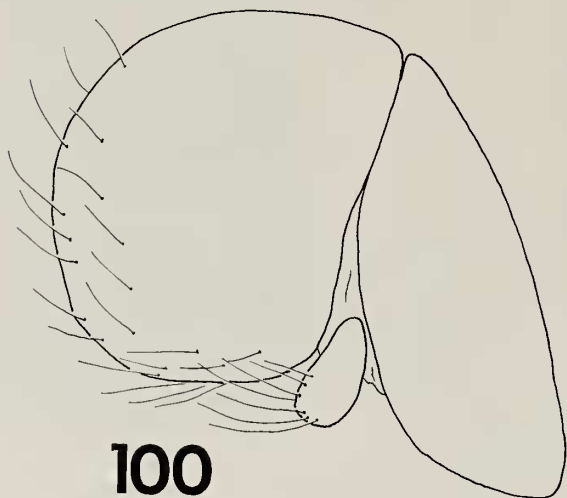
*Remarks.* — The record of *hispidipes* from Dixon Springs, Pope County, Illinois, by Causey (1950a), subsequently cited by Chamberlin and Hoffman (1958), actually refers to *oliphantus*. Since the types of *hispidipes* are from an unknown site in Illinois (Wood 1864, 1865) and *oliphantus* is the only species known from forested areas in the southern part of the state, it is frequently misidentified as the former. For example, I originally assumed that my specimen from Jackson County was *hispidipes*, but two species occur in this state. The prior confusion is understandable since no one has attempted to illustrate the apertures of the *hispidipes* syntypes, which have resided at the NMNH for a century and a quarter. To my knowledge they have not been examined since 1865, and in particular Causey (1950a) missed a golden opportunity to establish the identity of *hispidipes* by examining and illustrating them. Instead, she mistakenly assumed that the male of *oliphantus* from Dixon Springs (ILNHS) was *hispidipes*, so named it, and illustrated the mandibular process, the 2nd coxa, the aperture, a gonopod from lateral, not ventral, view, and the sternal projections between the 9th legs, 8th by her count. The aperture drawing from the lateral perspective does not show the pouches and is meaningless, so none of these drawings are definitive. Causey (1952a) provided a ventral view of the aperture showing the pouches and again, erroneously, labeled it *hispidipes*. Subsequent confusion can be traced to these mislabeled drawings, and when I examined the types of *hispidipes*, I was shocked to view a different form. I surmise that *hispidipes* is more common in central Illinois, where there has been little recent collecting, whereas *oliphantus* is abundant in the



96



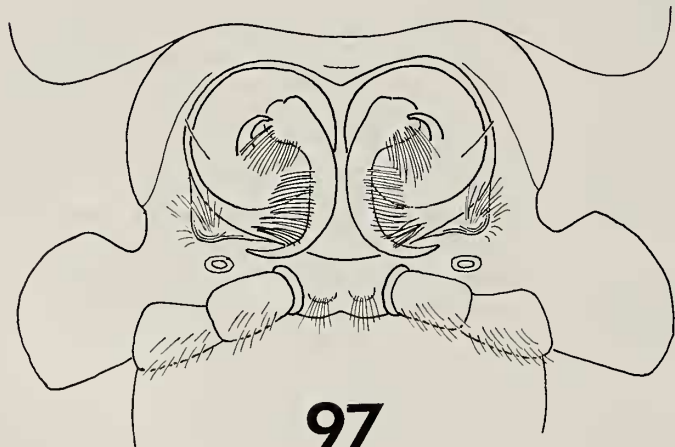
101



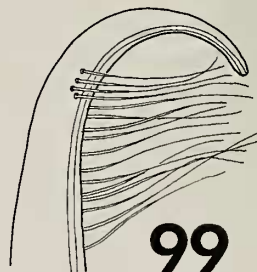
100



98



97



99

Figs. 96-101. *Eurymerodesmus elevatus*. 96, projection of right mandible of holotype, lateral view. 97, aperture and gonopods *in situ* of holotype, ventral view. 98, left gonopod of the same, lateral view. 99, telopodite of the same, medial view. 100, left cyphopod of female paratype, caudal view. 101, the same, medial view. Scale line for fig. 97 = 1.00 mm. Line for other figs. = 0.30 mm for 96, 0.40 mm for 98 and 100-101, and 0.50 mm for 99.



southern part of the state, in the mesic woodlands of the Shawnee National Forest.

*Eurymerodesmus oliphantus* is one of three species taken from caves, the others being *melacis* and *birdi*. As indicated later, *melacis* may seek refuge in caves, but *oliphantus* is surely an accidental species, since there is abundant, moist epigeal habitat in the Ozarks.

*Eurymerodesmus oliphantus* has the largest, most open caudolateral pouches in the family, so much so that they alone are diagnostic for the species.

### *Eurymerodesmus elevatus*, new species

Figs. 54, 96-101

*Type specimens*. — Male holotype and female paratype (FSCA) collected by W. W. Dowdy, 12 February 1966, on Neilhorn Place, Jefferson City, Cole Co., MO. Male paratype (NCSM) taken by same collector, 15 April 1965, on Lepage Place, Cole Co., presumably in Jefferson City.

*Diagnosis*. — A small to moderate-size species; males characterized by relatively short mandibular projection; sides of aperture divided, outer lateral margin rising beyond division point into cupped elevated lobe forming false pouch on inner surface; telopodite long; acropodite short, about 1/4 of the telopodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of female not modified, without projections; receptacle moderate-size, sides not curving around operculum.

*Color in life*. — Unknown.

*Holotype*. — Fragmented into three pieces, approximate length 19.2 mm, maximum width 3.2 mm, W/L ratio 16.7%.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.3 mm, interantennal isthmus 0.8 mm. Antennae reaching back to middle of 3rd tergite, relative lengths of antennomeres 2 > 3 > 5 > 6 > 4 > 1 > 7. Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 1-1, clypeal about 7-7, labral about 16-16. Process of mandibular stipes relatively short, subtriangular, apically blunt (Fig. 96).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum; posterior corners rounded through segment 10, blunt on 13-15, becoming progressively more acute caudally.

5th sternum with elevated flattened areas between 4th legs and larger paramedian knobs between 5th; 6th sternum with broad, elevated areas between both leg pairs. Postgonopodal sterna with slightly elevated, widely segregated hirsute areas between 9th legs; remaining sterna generally flat and unmodified, with variably impressed transverse grooves originating between leg pairs and hair

patches adjacent to leg coxae, becoming progressively sparser caudally. 2nd coxa with short, broadly triangular anterior, and minute caudal, lobes. Prefemora with broad lobes on outer surfaces of legs through segment 10.

Gonopodal aperture (Fig. 97) broadly ovoid, with open caudolateral pouches and short, broad anterior indentation, 1.6 mm wide and 0.7 mm long at maxima, outline of apparatus subrectangular; anterior indentation short, broad, subacuminate; sides divided, essentially upright, not leaning over opening, rising continuously from anterolateral corner to peak on outer lateral margin at caudolateral corner beyond division point, latter caudal to midlength, inner lateral margin continuing curvature of anterior part of sides, blending smoothly into inner caudal margin, outer lateral margin rising continuously into broad, elevated lobe at caudolateral corner, not flaring laterad, cupped with slight cavity on inner surface in conjunction with outer caudal margin, rims of anterior lateral margins slightly irregular, becoming more so on elevation; inner caudolateral corners smoothly curved, indistinct, continuous with inner lateral margin; outer caudolateral corners relatively sharp, nearly a right angle; inner caudal margin smoothly continuing curvature of sides, merging with outer caudal margin well before midline, at about 1/3 length; latter dropping rapidly from caudolateral corner to level of metazonum, angling inward and merging with inner caudal margin, the two then continuing as single, smoothly curved caudal margin across midline; anterior margin and anterior halves of sides essentially glabrous, a single hair arising from rim of latter, more hairs arising from rim of outer caudal margin on elevation beyond division point, with additional short hairs on outer surface of elevation and moderate tuft in pouch, caudal margin glabrous. Gonopods *in situ* (Fig. 97) with telopodites approaching each other in midline then curving broadly laterad across caudal margin, terminating over 9th coxal condyles, apices directed sublateral. Gonopod structure as follows (Figs. 98-99): Telopodite extending slightly beyond level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, bowed for most of length, more so distad, narrowing smoothly and continuously, with two rows of continuous, evenly spaced hairs along inner margin, angling outward distad, and distomedial tuft of four hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, poorly demarcated from, and smoothly continuous with, prefemur, smoothly continuing curvature of distal part of latter basally, flattening at midlength, becoming uncinately distally, narrowing continuously to acuminate tip.

*Female paratype*. — Body fragmented, length approximately 25.3 mm, maximum width 3.9 mm, W/L ratio 15.4%. Agreeing essentially with holotype in somatic features, with following exceptions: Mandibular stipes with minute, rounded, process. Sterna flat and nearly glabrous, with only a few scattered hairs.

Cyphopodal aperture subrectangular, sides slightly elevated above metazonal surface, caudal margin with moderate indentation at midpoint. Cyphopods *in situ* with edges of valves and tip of receptacle visible in aperture. Valves (Figs. 100-101) oriented transversely in aperture, relatively small, subequal, without projections or modifications, lightly hirsute on medial side. Receptacle located laterad to valves, relatively small, glabrous, sides not curving around operculum. Latter small, located under free, dorsal, side of valves.

*Male paratype*. — The male paratype agrees with the holotype in all particulars.

*Variation*. — The other Cole County males and females agree closely with the holotype and paratype, except that the gonopods *in situ* may cross

in the midline of the aperture and again over the caudal margin, or lie over and under one another in the midline. In the Morgan County male, the outer lateral margin is more strongly elevated and flares slightly laterad, thus forming a higher and slightly deeper pouch.

*Ecology.* — According to the vial label, the holotype and female paratype were collected "in soil." The male from the flood plain in Cole County was taken from the "first inch" presumably of the soil or leaf litter. There are no indications whether these sites were in forest, pasture, or other environments.

*Distribution.* — Known only from two counties in central Missouri (Fig. 54), the distance between known sites being only about 50 miles. Specimens were examined as follows:

MISSOURI: *Cole Co.*, Jefferson City, Neilhorn Pl., M, F, 12 February 1966, W. W. Dowdy (FSCA) TYPE LOCALITY; Lepage Pl., probably near Jefferson City, M, 15 April 1965, W. W. Dowdy (NCSM); flood plain without further data, M, 19 January 1968, W. W. Dowdy (FSCA); and along US hwy 54 in southern Cole Co., M, 2F, 25 October 1965, W. W. Dowdy (FSCA). *Morgan Co.*, Versailles, M, 12 April 1959, D. Zusteg (FSCA).

*Remarks.* — The specimens of *elevatus* were either broken when I obtained them or fragmented upon handling. All measurements are therefore approximations.

The cavity formed by the elevated outer lateral and caudal margins, the cupped inner surface of the elevation, is convergent with that of *impurus* in that the inner lateral margin forms the floor instead of the inner edge. It differs from the true pouches of other species in the *varius* group, but the hair tuft in the cavity and the uncinat acropodite, similar to that of *newtonus*, indicate that *elevatus* properly belongs here.

### The Simplex Group

The *simplex* group includes forms with short acropodites that are discontinuous with, and strongly demarcated from, the prefemur in all populations. It contains the fourth oldest species, *simplex*. The acropodite may be subterminal, with the distal extremity of the prefemur overhanging and extending beyond it, or narrowly terminal arising exclusively from the inner prefemoral margin, the outer surface of which projects above the junction and may be expanded or clavate but does not extend distad beyond the origin of the acropodite. Apertures vary, some

having divided lateral margins and pouches, as in *simplex*, *parvicus*, and *crassatus*, others having undivided sides and triangular lobes on the caudal margin as found in *birdi*, for example *polkensis* and *pulaski*, and still others exhibiting undivided sides without lobes, for example *caesariatus* and *serratus*. The *simplex* group occurs sporadically from Florida to Louisiana and western Arkansas. Most components are widely segregated, and *serratus* even has allopatric populations some 700 miles apart. Consequently, a number of undiscovered forms probably exist, particularly in southern Arkansas, northern Louisiana, and western Mississippi.

As stated previously, *varius*, with discontinuous acropodites in *v. christianus*, links the *simplex* and *varius* groups into a single natural assemblage. For convenience I separate them based on the degree of differentiation between the acropodite and prefemur, and the relative number of populations displaying this trait.

*Components:* *simplex* Chamberlin; *parvicus* (Chamberlin); *pulaski* (Causey); *polkensis* (Causey); *caesariatus*, new species; *crassatus*, new species; and *serratus*, new species.

### *Eurymerodesmus simplex* Chamberlin

Figs. 54, 102-107, 211

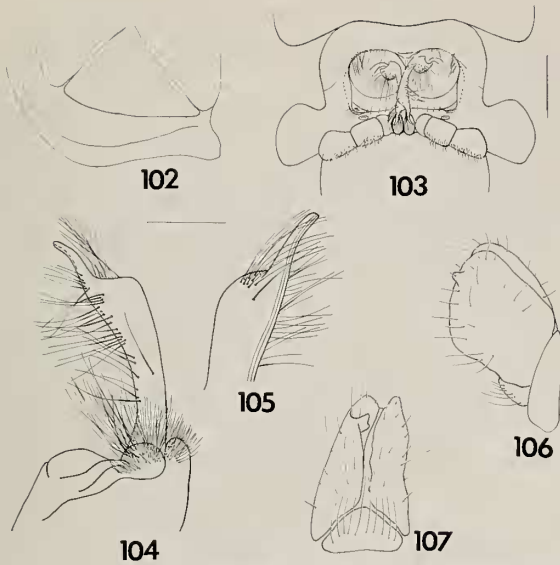
*Eurymerodesmus simplex* Chamberlin, 1920:98-99. Attems, 1938:187.

*Kewanus simplex*: Chamberlin and Hoffman, 1958:82.

*Type specimen.* — Male holotype (MCZ) and one male and one female paratype (NMNH) collected by H. E. Hubert on an unknown date in 1918 from an unknown locality in Louisiana. The labels in the vials and Chamberlin (1920) reported New Orleans as the type locality, but Chamberlin and Hoffman (1958) stated that the site was "probably near" this city and that no definite localities were known. Two other eurymerodesmids, *birdi planus* and *varius christianus* are known from New Orleans and environs, but the only definite sites for *simplex* are in Evangeline and Rapides Parishes, about 145 miles north northwest of the city. Thus, the type locality is unknown.

*Diagnosis.* — A moderate-size species; males characterized by short mandibular projection; sides of aperture divided, forming moderately open pouches; telopodite long; acropodite short, about 1/4 of telopodite length, narrowly terminal, arising solely from inner prefemoral margin; prefemur with moderate number of hairs arranged continuously along inner surface, expanding distad into broad,





Figs. 102-107. *Eurymerodesmus simplex*. 102, projection of right mandible of holotype, lateral view. 103, aperture and gonopods *in situ* of holotype, ventral view. 104, left gonopod of holotype, lateral view. 105, the same, medial view. 106, left cyphopod of female from Evangeline Par., LA, medial view. 107, the same, anterior view. Scale line for fig. 103 = 1.00 mm. Line for other figs. = 0.30 mm for 102, and 0.50 mm for 104-107.

clavate shoulder on outer margin; cyphopod valves of females with subterminal marginal spur on medial valve, distal corners not produced; receptacle small, sides not curving around operculum.

*Color in life.* — Unknown.

*Holotype.* — Body highly fragmented, length unmeasurable, maximum width 4.2 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.2 mm, interantennal isthmus 0.9 mm. Antennae reaching back to middle of 3rd tergite, relative lengths of antennomeres 2 > 3 > 4 > 6 > 5 > 1 > 7. Genae without impressions. Facial setae as follows: epicranial, interantennal, and subantennal absent, frontal 1-1, genal 1-1, clypeal about 8-8, labral about 14-14. Process of mandibular stipes short and broad, apically indented (Fig. 102).

Collum extending below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 6, blunt on 7-14, becoming progressively more acute beginning on segment 15.

5th sternum with low, rounded elevated areas between both leg pairs; 6th sternum with broad elevated areas between anterior legs and pair of long, conical, caudally directed projections between caudal legs, narrowly segregated in midline, longer than widths of adjacent coxae. Postgonopodal sterna with pair of broad knob-like processes between 9th legs, narrowly segregated in midline, apices angling anteriorly, lengths subequal to widths of adjacent coxae; remaining sterna with variably elevated areas between both leg pairs on segments 8 and 9, caudal ones longer and tapering medially, sterna becoming flatter and more plate-like with incomplete transverse impressions thereafter, with slight hair patches

adjacent to coxae. 2nd coxa with broad anterior, and sub-acuminate posterior, lobes. Prefemoral lobes continuing through segment 9.

Gonopodal aperture (Fig. 103) subrectangular, with slight caudolateral pouches and broad anterior indentation, 1.9 mm wide and 0.8 mm long at maxima, outline of apparatus rectangular; anterior indentation short, broadly rounded; sides divided, slightly wider anteriorly than narrowing, angling slightly medially, and elevating beyond division point to caudolateral corner, division point located caudal to midlength, just before caudolateral corner, inner lateral margin very short, heading directly into inner caudolateral corner and then into inner caudal margin; outer caudal margin rising slightly to outer caudolateral corner, forming slight, open pouch with inner margin, rims slightly irregular; inner caudolateral corner indistinct; outer caudolateral corner rounded but sharp, nearly a right angle; inner caudal margin merging with outer margin just beyond caudolateral corner; outer caudal margin very short, extending from corner directly into inner margin, the two then continuing in slight bisinuate curve across midline, flush with metazonal surface; margins irregularly hirsute, with long hairs arising from anterior margin, thickest at anterolateral corners, with denser tufts of short hairs in pouches and a few short stiff hairs from caudal margin. Gonopods *in situ* (Fig. 103) with telopodites angling medially and extending directly caudad, overlying each other in midline and projecting well beyond caudal margin, apices diverging over sternum between 9 legs. Gonopod structure as follows (Figs. 104-105): Telopodite terminating just before level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, leaning over coxa, expanding greatly beyond midlength into broad, clavate shoulder on outer margin, with two relatively sparse rows of continuous, but irregularly spaced hairs on inner margin to level of shoulder, culminating in a slight tuft, a distomedial tuft of about 12 hairs on shoulder at junction of acropodite, and one additional proximal hair on medial surface. Acropodite short and narrowly terminal, about 1/4 of telopodite length, arising from inner prefemoral margin, discontinuous with, and strongly demarcated from prefemur, much narrower than latter, bisinuate, apically blunt.

*Female from Evangeline Par.* — Approximate length 28.0 mm, maximum width 3.5 mm, W/L ratio 12.5%. Agreeing closely with holotype in somatic features, with following exceptions: Subantennal setae 1-1, genal 4-4. Mandibular stipes with short process, apically squared. Sterna relatively flat and unmodified, with variable, incomplete transverse impressions on all segments.

Cyphopodal aperture elliptical, sides and caudal margin elevated above metazonal surface. Cyphopods *in situ* with corners of valves protruding through aperture, open side facing anteriorly. Valves (Figs. 106-107) moderately large and moderately hirsute, unequal, lateral larger than medial, oriented dorsoventrally in aperture, medial valve with subterminal marginal spur, distal corners not produced. Receptacle relatively small, glabrous, located dorsad to valves on caudal side, not curving partly around operculum. Latter moderate-size, tucked under open (anterior) side of valves.

*Variation.* — The gonopods of all males are nearly identical to those of the holotype. The aperture varies slightly in that it does not lean as far over the opening in some individuals, thus forming a shallower, more open concavity. In the male from Rapides Parish the caudal margin is distinctly elevated across the midline. Hairs arise irregularly all along the lateral rims and down the outer surfaces on

specimens from Evangeline and Rapides parishes. The lobes between the 9th legs are similar to those on the holotype in the Rapides Parish male and one from Evangeline Parish. The other Evangeline male possesses enormous subconical projections, much longer than the widths of the adjacent coxae, and they lean anteriorly, thus displacing the apices of the telopodites. One lies between the lobes, and the other is pushed laterad over the coxa.

*Ecology.* — The Evangeline specimens were found under logs on a mixed pine-hardwood hillside.

*Distribution.* — Known definitely from the following two sites in central Louisiana (Figs. 54, 211).

LOUISIANA: *Rapides Par.*, Forest Hill, M, 11 October 1945, R. L. Wenzel (FMNH). *Evangeline Par.*, 0.25 mi. S Rapides Par. line near Cocodrie Bayou, 2M, 3F, 1 February 1968, E. D. Keiser (FSCA).

*Remarks.* — The males from Evangeline and Rapides Parishes were tightly coiled and broke into several pieces upon handling, rendering length measurements impossible. The female measurement is only an approximation. However, *simplex* is generally a moderate-size species, smaller than *goodi* and *dubius*, but considerably larger than *varius*.

In proposing *Kewanius* for *simplex* Chamberlin (1938) did not officially form the new combination. This was done 20 years later by Chamberlin and Hoffman (1958), and remains the only formal publication of *K. simplex*.

This species is the fourth oldest in the genus, and it has never been illustrated. Causey (1963) restudied the types, claimed to find no differences warranting a new genus, and synonymized *Kewanius* with *Eurymerodesmus*, all without publishing a word of description or any illustrations. When I first saw the holotype I was surprised to see the discontinuous acropodite and clavate prefemur, since none of the previous works alluded to them. After analyzing *Eurymerodesmus* as a whole, I agree that *Kewanius* is a synonym, but it is amazing that Causey (1963) was so unimpressed by these characters that she did not even consider them worth mention. The discontinuity is so striking, that without studying all eurymerodesmids, I think one would have to give credence to Chamberlin's generic name.

***Eurymerodesmus polkensis* (Causey),  
new combination**

Figs. 54, 108-115, 211

*Paresmus polkensis* Causey, 1952b:5, fig. 4. Chamberlin and Hoffman, 1958:83.

*Type specimen.* — Male holotype (AMNH) collected by N. B. Causey, 6 September 1950, 11 mi. N Mena, Polk Co., AR.

*Diagnosis.* — A large species; males characterized by large, broad mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating continuously, extending around caudolateral corners into moderately large, broadly rounded lobes on caudal margin; telopodite long; acropodite short, about 1/8 of telopodite length, narrowly terminal, arising from inner prefemoral margin; prefemur with many hairs arranged continuously along inner surface, not expanding distad, without detectable shoulder; females unknown.

*Color in life.* — Paranota red-orange; metaterga dark olive, prozonites darker, with red-orange "medial triangles" (Causey 1952b). None of the available specimens show evidence of color pattern, but from Causey's remarks, the species apparently displays middorsal spots instead of stripes.

*Holotype.* — Body highly fragmented, length unmeasurable, maximum width 6.6 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 3.0 mm, interantennal isthmus 1.1 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres  $2 > 5 > 6 > 3 > 4 > 7$ . Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, subantennal, and genal absent, frontal 1-1, clypeal about 12-12, labral about 18-18. Process of mandibular stipes broad, heavily sclerotized, apically blunt (Fig. 108).

Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 8, blunt on 9-14, becoming progressively more acute caudally.

5th sternum with knob-like projections between both leg pairs, those between caudal (5th legs) larger and more widely segregated; 6th sternum with larger projections, those between caudal (7th) legs more widely separated. Postgonopodal sterna with short, knob-like processes between 9th legs; remaining sterna with lower elevations on segments 8-9, becoming progressively flatter and more sparsely hirsute caudally. 2nd coxa with strong subconical anterodistal, and short rounded posterior, lobes. Prefemoral lobes extending through segment 16.

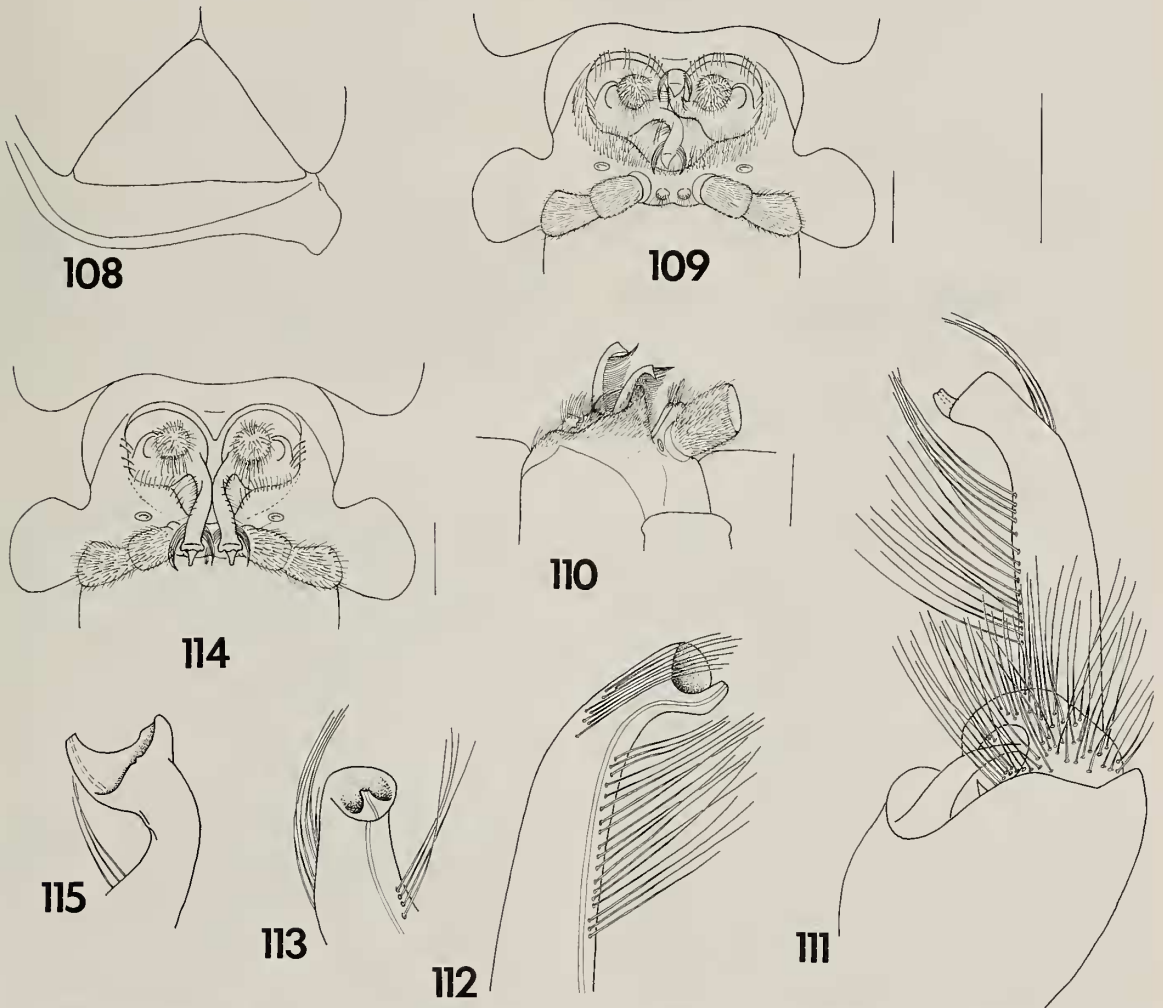
Gonopodal aperture (Fig. 109, not this specimen) subrectangular, without caudolateral pouches, with strong anterior indentation, 2.7 mm wide and 1.0 mm long at maxima; anterior indentation long, triangular, acuminate; sides not divided, almost linear, curving very slightly caudomedial, elevating smoothly and continuously around caudolateral corner onto caudal margin, leaning only very slightly over opening, rims smooth; caudolateral corners rounded, obtuse; caudal margin continuing elevation of sides laterally, extending rapidly into moderately large, broadly rounded lobes (Fig. 110), tapering rapidly to metazonal surface and extending caudad in midline; margins densely hirsute, with tufts apically and along sides of anterior indentation, sporadic hairs along anterior margin, becoming progressively denser caudally along sides on rims and outer surfaces, densest on caudal lobes,



narrowing into a row along caudal midline. Gonopods *in situ* (Fig. 114, not this specimen) with telopodites abutting or overlying each other in midline of aperture, diverging, extending over caudal margin, and terminating over sternum between 9th legs. Gonopod structure as follows (Figs. 111-113): Telopodite terminating before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite length, sublinear and of nearly uniform width for most of length, narrowing distad and curving dorsad, with slight cavity on apical margin, with two rows of continuous, regularly spaced hairs along inner surface and distomedial tuft of about 10 hairs. Acropodite short and narrowly terminal, about 1/8 of telopodite length, arising from inner distal margin of prefemur, discontinuous with, and sharply demarcated from latter, curving slightly ventrad, apically blunt.

*Variation.* — The male from Scott County measures 39.4 mm in length, 6.2 mm in width, W/L

ratio 15.7%. The lobes on the caudal margin of the aperture appear slightly smaller than those of the type, and the caudal margin extends farther caudad in the midline. The left gonopod was displaced and directed ventrad rather than caudad (Fig. 109). The unbroken specimen from Montgomery County measures 33.7 mm long, 5.4 mm wide, W/L ratio 16.0%. The lateral margins of the aperture are more strongly elevated, and the lobes are distinctly higher but markedly less hirsute. On the gonopods the prefemur is bent more strongly distad, and the acropodite extends around the distal extremity of the prefemur and is expanded and cupped to form a definite terminal calyx (Fig. 115) with irregular margin.



Figs. 108-115. *Eurymerodesmus polkensis*. 108, projection of right mandible of holotype, lateral view. 109, aperture and gonopods *in situ* of male from Scott Co., AR, ventral view. 110, the same, lateral view. 111, left gonopod of holotype, lateral view. 112, telopodite of the same, medial view. 113, apex of the same, ventral view. 114, aperture and gonopods *in situ* of male from Montgomery Co., AR, ventral view. 115, apex of telopodite of left gonopod of the same, lateral view. Scale lines for figs. 109-110 and 114 = 1.00 mm. Line for other figs. = 0.30 mm for 108 and 111, 0.40 mm for 112, and 0.50 mm for 113 and 115.

*Ecology.* — Notations on the vial labels indicate that the male from Scott County was taken on a wooded hillside; those from Montgomery County were discovered in a "pig dung trap."

*Distribution.* — Known only from three adjacent counties in western Arkansas (Figs. 54, 211). Specimens were examined as follows:

ARKANSAS: *Scott Co.*, 4 mi. W Y City, M, 24 October 1963, L. Hubricht (RLH). *Polk Co.*, 11 mi. N Mena, M, 6 September 1950, N. B. Causey (AMNH) TYPE LOCALITY. *Montgomery Co.*, Muddy Cr. Wildlife Management Area, along US hwy. 270, 5.2 mi. W Pencil Bluff, 2M, 6-8 March 1977, R. E. Woodruff (FSCA).

*Remarks.* — *Eurymerodesmus polkensis* is placed in the *Kewanius* lineage, *simplex* group, because of the discontinuous prefemora, but it could equally well go in the *birdi* lineage because of the undivided aperture sides, the absence of pouches, and the distinct lobes on the caudal margin. By combining the aperture of *birdi* with the *simplex*/*varius* gonopod, *polkensis* proves that the undivided/lobed-divided/pouch aperture extremes are congeneric.

### *Eurymerodesmus caesariatus*, new species

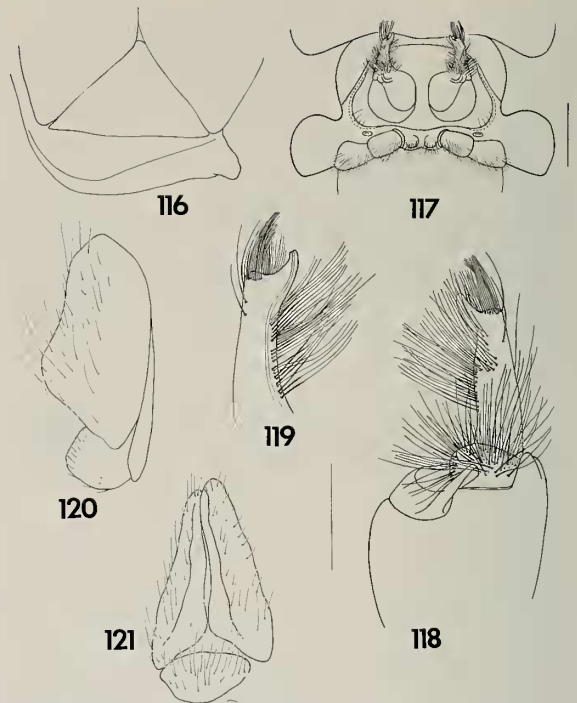
Figs. 54, 116-121

*Type specimens.* — Male holotype and one female and one juvenile paratype (FSCA) collected by N. B. Causey, 23 December 1953, 7 mi. N Meadville, Franklin Co., MS.

*Diagnosis.* — A moderate-size species; males characterized by moderately long mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating slightly, continuing around caudolateral corner, and tapering rapidly to metazonal surface a short distance onto caudal margin; telopodite short, extending directly ventrad not caudad, wholly enclosed within aperture; acropodite short, about 1/4 of telopodite length, arising solely from inner prefemoral margin; prefemur not expanding distad, without detectable shoulder, with many hairs arranged continuously along inner surface and dense terminal corona lying parallel to acropodite; cyphopod valves of females moderately large, distal corners slightly elongate; receptacle narrow, sides not curving around operculum.

*Color in life.* — Unknown. The blanched types lack any trace of either color or pattern.

*Holotype.* — Length 27.0 mm, maximum width 4.2 mm, W/L ratio 15.6%.



Figs. 116-121. *Eurymerodesmus caesariatus*. 116, projection of right mandible of holotype, lateral view. 117, aperture and gonopods *in situ* of holotype, ventral view. 118, left gonopod of holotype, lateral view. 119, telopodite of the same, medial view. 120, left cyphopod of female paratype, medial view. 121, the same, anterior view. Scale line for fig. 117 = 1.00 mm. Line for other figs. = 0.30 mm for 116, 0.40 mm for 118 and 120-121, and 0.50 mm for 119.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.4 mm, interantennal isthmus 0.6 mm. Antennae reaching back to just beyond caudal margin of 2nd tergite, relative lengths of antennomeres 2>3>4>5=6>1>7. Genae without impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent, subantennal 1-1, clypeal about 8-8, labral about 14-14. Process of mandibular stipes moderately long, apically blunt (Fig. 116).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 10, blunt on 11-14, becoming progressively more acute caudally.

5th sternum with short, subequal, knob-like projections between leg pairs, those between caudal (5th) legs more widely separated; 6th sternum with similar knobs between anterior legs and broad, flattened, elevated areas between caudal legs. Postgonopodal sterna with low, densely hirsute, knob-like processes between 9th legs; remaining sterna with hirsute elevated areas on segments 8-10, becoming progressively flatter, more plate-like, and less hirsute caudally, caudalmost sterna glabrous or nearly so. 2nd coxa with short, conical anterior, and minute rounded caudal, lobes. Prefemoral lobes extending through legs on segment 10.

Gonopodal aperture (Fig. 117) broadly trapezoidal, without caudolateral pouches and anterior indentation, 1.5 mm wide and 0.8 mm long at maxima; anterior margin without trace of indentation; sides not divided, angling caudolaterad, elevating impercep-



tibly to caudolateral corner, not leaning over opening, rims smooth; caudolateral corner broadly rounded; caudal margin continuing elevation of sides laterally, tapering rapidly to metazonal surface, extending slightly caudad in midline; margins almost glabrous, with only very few hairs on caudolateral corners. Gonopods *in situ* (Fig. 117) with telopodites extending nearly directly ventrad, in parallel arrangement, completely enclosed by opening, oriented vertically and perpendicular to body axis, not extending caudad. Gonopod structure as follows (Figs. 118-119): Telopodite relatively short, terminating well before level of distal extremities of hairs. Prefemur long, about 3/4 of telopodite length, configuration linear, widening beyond midlength then narrowing distad, with two dense rows of continuous, regularly spaced hairs along inner margin, additional hairs between rows, and dense terminal marginal tuft of 16 or so very broad hairs lying parallel to and obscuring acropodite, and forming corona. Acropodite short and narrowly terminal, about 1/4 of telopodite length, obscured by terminal prefemoral hairs, arising from inner margin of distal extremity of prefemur, discontinuous with, and sharply demarcated from, latter, curving slightly ventrad, apically rounded.

*Female paratype.* — Body highly fragmented, length unmeasurable, maximum width 3.9 mm. Somatic features agreeing essentially with holotype, with following exceptions: Process of mandibular stipes minute, rounded, barely projecting from stipital surface. 3rd sternum with two minute, hirsute lobes, remaining sterna flat and essentially glabrous.

Cyphopodal aperture subrectangular, sides elevated above metazonal surface. Cyphopods *in situ* with corners of valves protruding through aperture, valves oriented along body axis. Valves (Figs. 120-121) relatively large, subequal, distal corners slightly prolonged and rounded, moderately hirsute. Receptacle narrow, located on caudal surface of valves, closely adhering to latter, sides not curving partly around operculum. Latter comparatively large, clearly visible under free, anterodorsal corner of valves.

*Ecology.* — Unknown.

*Distribution.* — Known only from the type locality (Fig. 54).

*Remarks.* — The terminal prefemoral hairs are packed so tightly that they superficially resemble a sclerotized lamella; at first glance there appeared to be a terminal clayx. They form a semicircular corona and I think are homologous to the distomedial tuft on other species, which is situated more on the medial surface a short distance from the end of the prefemur.

In general configuration, the telopodite of *caesariatus* is closest to that of *polkensis*. However, *caesariatus* occurs some 280 miles southeast of *polkensis*, so the intervening part of Arkansas and Louisiana probably contains other forms with narrower terminal acropodites.

***Eurymerodesmus paroicus* (Chamberlin),**

new combination

Figs. 54, 122-125, 211

*Paresmus paroicus* Chamberlin, 1942a:7, pl. 2, figs. 18-19. Chamberlin and Hoffman, 1958:82.

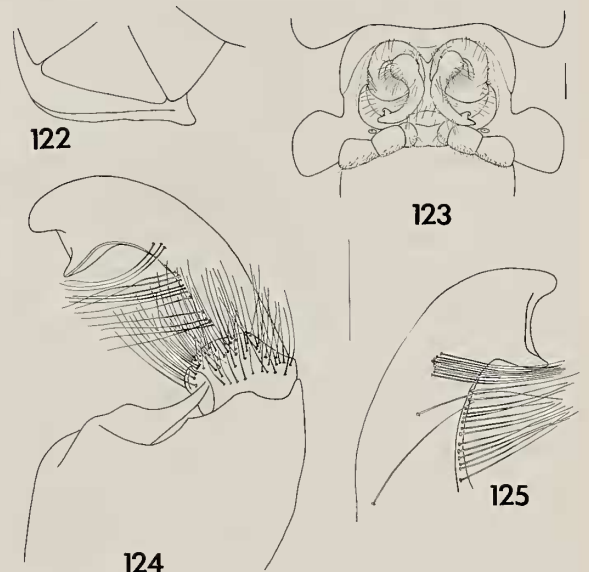
*Type specimen.* — Male neotype and one additional male (FSCA) collected by W. J. Harmon, December 1954, 900 S. Farmerville St., Ruston, Lincoln Par., LA. This site is around 5-6 miles north of the type locality, 1.5 mi. N Clay, at the border of Lincoln and Jackson Parishes. The type vial, containing the original label, is at the NMNH, but it contains four males of *Pseudopolydesmus pine-torum* (Bollman) and not even a loose eurymerodesmid segment. Thus the type series, containing the holotype and an unknown number of paratypes, is lost.

*Diagnosis.* — A moderate to large species; males characterized by short mandibular projection; sides of aperture divided, forming shallow open pouches; telopodite long; acropodite short, about 1/8 as long as prefemur arising subterminally from inner prefemoral margin; prefemur very long and very broad, comprising entire length of telopodite, with rounded, glabrous, distal lobe overhanging and extending beyond level of acropodite and with modest number of hairs arranged continuously along inner margin to near base of acropodite, inner surface smooth, not excavated; females unknown.

*Color in life.* — Unknown.

*Neotype.* — Body highly fragmented, length unmeasurable, maximum width 4.0 mm.

Somatic features similar to *hispidipes*, with following exceptions:



Figs. 122-125. *Eurymerodesmus paroicus*. 122, projection of right mandible of neotype, lateral view. 123, aperture and gonopods *in situ* of neotype, ventral view. 124, left gonopod of the same, lateral view. 125, telopodite of the same, medial view. Scale line for fig. 123 = 1.00 mm. Line for other figs. = 0.13 mm for 122, 0.40 mm for 124, and 0.50 mm for 125.

Width across genal apices 2.6 mm, interantennal isthmus 0.9 mm. Antennae reaching back to caudal margin of 3rd tergite, relative lengths of antennomeres 2>4>3>5>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial 1-1, interantennal and frontal absent, subantennal 1-1, genal 4-4, clypeal about 10-10, labral about 13-13. Mandibular stipes with short, narrowly rounded projection (Fig. 122).

Collum not extending below ends of following tergite. Paranota moderately flattened, interrupting slope of dorsum; posterior corners blunt on anterior segments, becoming progressively prolonged and acute posteriorly.

Sternum of segment 5 with broad, flattened, elevated areas between both pairs of coxae, caudal elevations (between 5th legs) higher and more segregated in midline; 6th sternum with elevations stronger, more rounded, and more densely hirsute, caudal ones (between 7th legs) higher. Postgonopodal sterna with low, widely segregated lobes between 9th legs; remaining sterna becoming progressively flatter and more plate-like posteriorly, with slight hirsute lobes adjacent to coxae on segments 8 and 9, tapering into hirsute patches on 10-11, becoming less dense caudally, with variably impressed transverse grooves originating between leg pairs. 2nd coxa with strong, conical anterior, and shorter rounded posterior, lobes. Prefemoral lobes extending through anterior legs of segment 12.

Gonopodal aperture (Fig. 123) broadly rectangular, with narrow, open caudolateral pouches and strong anterior indentation, 2.8 mm wide and 1.7 mm long at maxima, outline of apparatus subtrapezoidal; anterior indentation long, triangular apically acute; sides divided, curving slightly mediad, rising to division point caudal to midlength and leaning imperceptibly over opening, inner lateral margin plunging directly dorsad into opening then curving broadly into inner caudolateral corner, outer lateral margin upright, well separated from inner, flaring caudolaterad and dropping slightly to caudolateral corner, forming shallow open pouch with inner margin, rims slightly irregular; inner caudolateral corner broad, rounded, visible deep inside opening; outer caudolateral corner broadly rounded but approximately 90°; inner caudal margin curving smoothly across midline well inside opening, generally invisible; outer caudal margin dropping slightly from caudolateral corner to metazonal surface, running along anterior surfaces of coxal condyles, extending slightly caudad in midline; margins moderately hirsute with long hairs arising sporadically from rims and overhanging opening, slightly denser on anterior indentation, much denser at division points on sides, with relatively sparse growths from pouches evenly dispersed; caudal margin with a few widely separated hairs. Gonopods *in situ* (Fig. 123) with telopodites diverging and angling caudolaterad over inner caudal margin of aperture, acropodites directed dorsad. Gonopod structure as follows (Figs. 124-125): Telopodite terminating at level of distal extremities of hairs. Prefemur very long and broad, comprising entire length of telopodite, distal third glabrous, curving gently and leaning over coxa, curve increasing distad, terminating in broadly rounded lobe overhanging and extending beyond level of acropodite, of nearly subequal width throughout, narrowing slightly distad, with ridge along inner surface demarcating prostatic groove, with two rows of subcontinuous hairs along inner margin terminating proximal to origin of acropodite, distolateral tuft of 3 hairs, dense distomedial tuft of about 9-12 hairs, and 2 long proximal hairs on medial surface. Acropodite short, about 1/8 as long as prefemur, profile subtriangular, arising subterminally on inner surface of prefemur, sides narrowing rapidly to subacuminate tip, directed dorsad.

*Variation.* — All males of *paroicus* are frag-

mented beyond the point where they can be re-assembled for measurements. The only noticeable variation is slight differences in the alignment of the lateral aperture margins. They are linear in the neotype, angled slightly caudolaterad in another male, and bowed slightly in the others. The last two conditions result in slightly larger pouches.

*Ecology.* — According to Chamberlin (1942a), the type series was encountered under logs.

*Distribution.* — Known only from Lincoln Parish, Louisiana (Figs. 54, 211). Specimens were examined as follows:

LOUISIANA: *Lincoln Par.*, Ruston, 900 S. Farmerville St., 2M, December 1954, W. J. Harmon (FSCA) NEOTYPE; and unknown location in Ruston, 2M, October and November 1951, collectors unknown (FSCA).

*Remarks.* — The gonopod of *paroicus* is one step removed from the condition in *polkensis*. If the apex of the latter's prefemur were swollen and extended slightly beyond the acropodite, the two would be practically interchangeable except for the slightly greater thickness of *paroicus*. However, the apertures are entirely different. That of *paroicus* has divided lateral margins and caudolateral pouches, whereas that of *polkensis* displays undivided sides and caudal lobes.

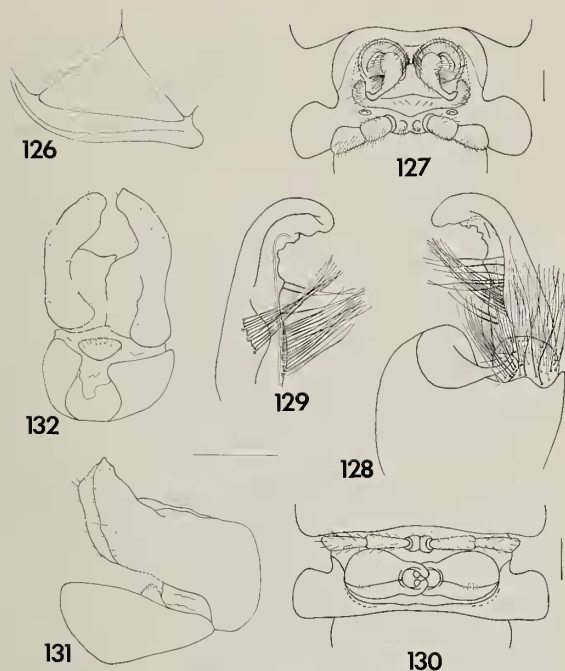
#### *Eurymerodesmus crassatus*, new species

Figs. 54, 126-132, 211

*Type specimens.* — Male holotype and 6 male and 2 female paratypes (FSCA) collected by L. D. Wilson, 24 March 1966, off old US highway 165, 2.6 mi. S Georgetown, Grant Par., LA. One male and one female paratype deposited in NCSM.

*Diagnosis.* — A moderate to large species; males characterized by short mandibular projection; sides of aperture divided, with open caudolateral pouches; telopodite long; acropodite minute, no more than 1/10 as long as prefemur, nubbinlike, arising subterminally from inner prefemoral margin; prefemur very long and very broad, comprising entire length of telopodite, with broad distal lobe overhanging and extending well beyond level of acropodite, with modest number of hairs arranged continuously along inner margin to near base of acropodite, inner surface emarginate; cyphopod valves of females with bowed projections from distal corners, apices touching or nearly so; receptacle moderate-size, sides curved partly around operculum.





Figs. 126-132. *Eurymerodesmus crassatus*. 126, projection of right mandible of holotype, lateral view. 127, aperture and gonopods *in situ* of paratype, ventral view. 128, left gonopod of the same, lateral view. 129, telopodite of the same, medial view. 130, cyphopods *in situ*, ventral view of female paratype. 131, left cyphopod of the same, caudal view. 132, the same, medial view. Scale lines for figs. 127 and 130 = 1.00 mm. Line for other figs. = 0.35 mm for 126 and 131, 0.40 mm for 128, and 0.50 mm for 129 and 132.

**Color in life.** — Unknown. The specimens are uniformly tawny after 23 years in alcohol and exhibit no trace of either color or pattern.

**Holotype.** — Length 25.0 mm, maximum width 4.1 mm, W/L ratio 16.4%.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.7 mm, interantennal isthmus 0.8 mm. Antennae reaching back to middle of 3rd tergite, relative lengths of antennomeres  $2 > 3 > 5 > 4 > 6 > 1 > 7$ . Genae with faint central impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 9-9, labral about 16-16. Process of mandibular stipes short, broadly rounded (Fig. 126).

Collum extending slightly below ends of following tergite. Paranota moderately depressed, somewhat interrupting slope of dorsum, peritremata flattened; posterior corners rounded through segment 3, blunt on 4-10, becoming progressively more acute caudally.

5th sternum with narrowly rounded, slightly elevated areas between both coxae; 6th sternum with broader, higher, flattened areas between coxae. Postgonopodal sterna with low, rounded elevations between 9th coxae; remaining sterna becoming progressively flatter and more plate-like caudally, with sparsely hirsute patches adjacent to coxae. 2nd coxa with moderately large, broad-

ly rounded anterior lobe and slightly shorter, subacute caudal one. Prefemoral lobes present on all but ultimate two leg pairs.

Gonopodal aperture (Fig. 127, not this specimen) broadly ovoid, with open caudolateral pouches and strong anterior indentation, 2.4 mm wide and 1.1 mm long at maxima, outline of apparatus broadly trapezoidal; anterior indentation long, triangular; sides curving gently mediad and leaning progressively over opening, rising to division point caudal to midlength, inner lateral margin exposed, extending nearly directly dorsad, curving strongly into inner caudolateral corner, outer lateral margin curling sharply dorsolaterad, not obscuring inner margin, dropping to outer caudolateral corner, forming shallow, open pouch with inner margin; inner caudolateral corner comparatively sharp, approximately a right angle; outer caudolateral corner broadly rounded; inner caudal margin flush with metazonal surface, extending slightly inward into opening; outer caudal margin dropping to metazonal surface shortly after outer caudolateral corner, extending caudad in midline; margins moderately hirsute, with tufts of 8 or so hairs on sides of anterior indentation, regularly spaced hairs along rest of anterior margin and sides to division point, moderate tufts in pouches, and scattered hairs between caudal margins. Gonopods *in situ* (Fig. 127, not this specimen) with telopodites widely separated and diverging, extending caudolaterad over inner caudal margin, apices curving sublateral. Gonopod structure as follows (Figs. 128-129): Telopodite essentially terminating at level of distal extremities of hairs. Prefemur very long, comprising entire length of telopodite, distal third glabrous, extending linearly for most of length, curving broadly distad and overhanging and extending well beyond level of acropodite in broadly rounded terminal lobe, very broad basally, widening into broad shoulder on medial surface near midlength, narrowing thereafter and tapering to broadly rounded tip, inner surface emarginate, with row of subcontinuous hairs on inner surface extending to just beyond shoulders and dense distal tufts of 15 or so hairs on lateral and medial surfaces of shoulders, latter located slightly distal to former. Acropodite minute and indistinct, a short, nubbinlike extension of inner surface of prefemur near base of distal curvature, no more than 1/10 as long as prefemur.

**Female paratype.** — Length 23.2 mm, maximum width 4.0 mm, W/L ratio 17.2%. Agreeing closely with males in structural details, with following exceptions: Process of mandibular stipes short, subacute.

Cyphopodal aperture broadly ovoid, sides strongly elevated above metazonal surface. Cyphopods *in situ* with edges of valves and projections visible in aperture (Fig. 130). Valves (Figs. 131-132) large, subequal, oriented transversely in aperture, leaning over receptacle, distal corners extending into broad, digitiform lobes, curving towards each other with apices touching or nearly so, with scattered hairs on projections. Receptacle relatively large, glabrous, located directly beneath valves, sides cupped partly around operculum. Latter small, hidden beneath, and obscured by, valves.

**Male paratypes.** — The male paratypes agree with the holotype in all particulars.

**Ecology.** — The types were taken at an old mill site, but the habitat is not indicated on the vial label.

**Distribution.** — Known only from the type locality.

**Remarks.** — This species is similar to *parvicus*, and future collecting in the gap of around 40 miles may show them to connect and be geographic races.

The apertures are very close, and the major differences involve the much shorter acropodite and irregular inner margin of *crassatus*.

The female is suspiciously similar to those of *angularis* in the valvular projections and may actually be referable to this species, occurring only two counties to the east. However, the position of the valves directly above the receptacle (Fig. 131) is unique, so it may be conspecific with the males.

***Eurymerodesmus pulaski* (Causey),  
new combination**

Figs. 54, 133-140, 211

*Leptodesmus hispidipes*: Bollman, 1888a:2, in part.

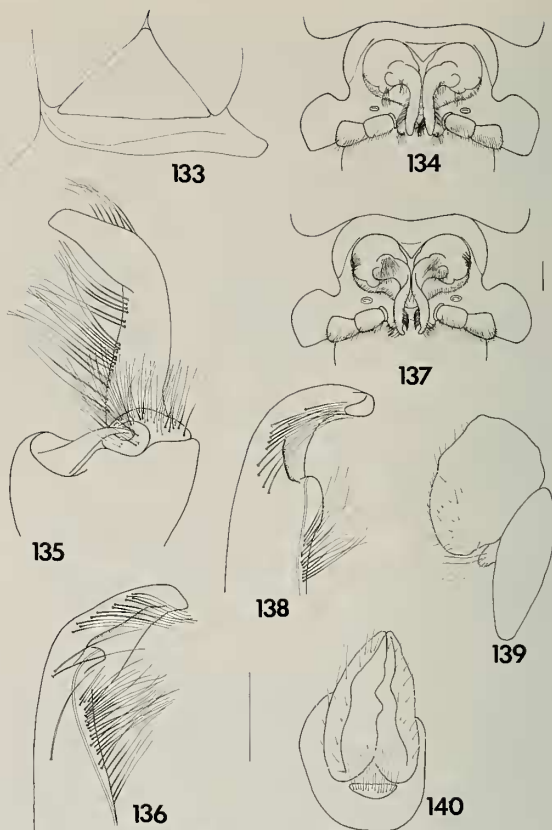
*Paresmus pulaski* Causey, 1950a:271-272, fig. 9; 1952b:4-5.  
Chamberlin and Hoffman, 1958:83.

**Type specimen.** — Male neotype, two additional males, and one female (NMNH) collected by C. H. Bollman, on an unknown date in the 1880's before 1888, at Little Rock, Pulaski Co., AR. The type locality, 3 mi. S Sweet Home, is on the southern periphery of Little Rock, and the type series consisted of two males collected in 1949. The holotype, reportedly at the ANSP (Causey 1950a, Chamberlin and Hoffman 1958), and the paratype, retained in Causey's private collection (Causey 1950a), now at the FSCA, are lost.

**Diagnosis.** — A moderate to large species; males characterized by long mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating slightly, curving around caudolateral corners, with suggestion of lobe on caudal margin; telopodite long, acropodite minute, less than 1/10 as long as prefemur, a blunt spur arising subterminally from inner prefemoral margin and situated in cavity in latter; prefemur very long and broad, comprising entire length of telopodite, expanding at level of acropodite into hood overhanging and shielding latter, broadly sublinear or distally uncinuate, with cavity on inner margin and many hairs arranged continuously along inner surface; cyphopod valves of females not modified, distal corners not extended; receptacle moderately large, sides expanding but not curving around operculum.

**Color in life.** — Paranota orange; metaterga dark olive, prozonites darker, with orange stripes along caudal margins connecting paranotal markings, expanding slightly mediad; collum with stripes on anterior and posterior margins (Causey 1950a).

**Neotype.** — Body highly fragmented, length unmeasurable, maximum width 5.2 mm.



Figs. 133-140. *Eurymerodesmus pulaski*. 133, projection of right mandible of neotype, lateral view. 134, aperture and gonopods *in situ* of neotype, ventral view. 135, left gonopod of the same, lateral view. 136, telopodite of the same, medial view. 137, aperture and gonopods *in situ* of male from Pulaski Co., AR, ventral view. 138, apex of telopodite of left gonopod of the same, medial view. 139, left cyphopod of female from Pulaski Co., lateral view. 140, the same, medial view. Scale lines for figs. 134 and 137 = 1.00 mm. Line for other figs. = 0.25 mm for 133, 0.37 mm for 135, 0.40 mm for 139-140, and 0.50 mm for 136 and 138.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 3.2 mm, interantennal isthmus 0.8 mm. Antennae reaching back to middle of 3rd tergite, relative length of antennomeres 2 > 3 > 4 > 6 > 5 > 1 > 7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, subantennal, frontal, and genal absent, clypeal about 10-10, labral about 15-15. Process of mandibular stipes long, subconical, tapering to blunt tip (Fig. 133).

Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 5, blunt on 6-11, becoming progressively more acute posteriorly. 2nd coxa with moderate-size subconical anterior lobe, caudal lobe only slightly smaller. Prefemoral lobes extending through segment 10.

Gonopodal aperture (Fig. 134) broadly ovoid, without caudolateral pouches, with strong anterior indentation, 2.7 mm wide and 1.0 mm long at maxima; anterior indentation long, triangular, acute; sides not divided, curving gently mediad, rising very slightly to caudolateral corner, not leaning over opening, rims



smooth; caudolateral corner broadly rounded, slightly elevated, forming a slightly obtuse angle; caudal margin rising slightly into suggestion of lobe then tapering to metazonal surface, extending caudad in midline; anterior margin glabrous, hairs beginning at midlength of sides and continuing onto caudal margin, regularly spaced. Gonopods *in situ* (Fig. 134) with telopodites extending caudad in parallel arrangement, extending well beyond aperture, overhanging sternum between 9th legs, apices directed dorsad. Gonopod structure as follows (Figs. 135-136): Telopodite terminating near level of distal extremities of hairs. Prefemur long, comprising entire length of telopodite, configuration slightly bisinuate, bending strongly dorsad distally, narrow basally, expanding beyond midlength into concave hood shielding acropodite, narrowing distad, apically blunt, with cavity on inner surface of hood, two rows of continuous, subregularly spaced hairs on inner surface to near distal bend, tuft of around 10 hairs on inner surface just before distal bend, distomedial tuft of around 10 hairs on hood, and 4 or so scattered hairs proximally on medial margin. Acropodite minute, a blunt subtriangular spur located subterminally in cavity on undersurface of hood at level of distal bend, partly shielded by sides of hood.

*Female from Pulaski Co.* — Body highly fragmented, length unmeasurable, maximum width about 4.5 mm. Process of mandibular stipes short, truncate. Other somatic features unknown because of great fragmentation and mixture of male and female segments in sample; impossible to reliably segregate segments by sex.

Cyphopodal aperture ovoid, sides flush with metazonal surface. Cyphopods *in situ* with edges of valves visible in aperture. Valves (Figs. 139-140) moderate-size, subequal, oriented transversely in aperture, medial (open) side densely hirsute, corners not extended. Receptacle moderately large, glabrous, located laterad at bases of valves, sides expanding beyond latter but not cupped around operculum. Latter small, located under free (open) end of valves.

*Variation.* — The neotype was chosen because it is the only available male matching Causey's illustration (1950a, fig. 9) of the holotype; it may have come from the same general area in south Little Rock. The NMNH sample contains fragments of two different males that may occur sympatrically in Little Rock. One exhibits sufficient gonopodal similarities to the neotype to be considered conspecific, but the other is so different as to require another binomial, and is therefore described in the ensuing account. The female in this sample may well be assignable to the following species, the other samples of which contain only males. There being no way this can be determined at present, I arbitrarily assign it to *pulaski*.

The acropodite of the variant is rudimentary, a thickened boss barely elevated above the prefemoral surface (Fig. 138). The cavity on the undersurface of the prefemur is very deep; the hood curves well over the acropodite as in the neotype; and the tip curls mediad to a subacuminate tip. The aperture configuration is the same, but the elevations on the caudal margin are higher, more distinctly lobe-like, and more densely hirsute (Fig. 137).

*Ecology.* — The type series was taken in an oak-pine association (Causey 1950a).

*Distribution.* — Known only from Pulaski County, Arkansas (Fig. 54, 211). The neotype and the associated males are the only available specimens.

*Remarks.* — Because of the high fragmentation of the Bollman and Hutcherson samples, it is impossible to determine which segment is which and thus to report the conditions of the sterna.

The neotype is one of Bollman's original samples and the label is in his handwriting. Consequently, this is probably one of the species he (1888a) identified as "*Leptodesmus hispidipes*" and stated was very common throughout Arkansas.

Pulaski County, and the area around Little Rock specifically, need to be meticulously sampled, since at least three forms occur there. At this writing I cannot determine if they are sympatric or parapatric; Bollman could well have combined samples from distant sites in the county under the general heading of Little Rock.

#### *Eurymerodesmus serratus*, new species Figs. 54, 141-146, 211

*Leptodesmus hispidipes*: Bollman, 1888a:2, in part.

*Type specimen.* — Male holotype (FSCA) collected by "Coffee," 11 October 1955, at Cato, Pulaski Co., AR. Male paratype (FSCA) collected G. B. Edwards, 4 November 1978, ca. 10 mi. SE Gainesville, along FL hwy. 325, 4 mi. S jct. FL hwy. 20, Alachua Co., FL.

*Diagnosis.* — A moderate to large species; males characterized by long mandibular projection; sides of aperture not divided, without caudolateral pouches, rising gradually to short lobe at caudolateral corners, caudal margin descending rapidly to metazonal surface; telopodite long; acropodite minute, less than 1/10 as long as prefemur, arising subterminally from inner prefemoral margin at base of expansion, situated in cavity in latter; prefemur very long, comprising entire length of telopodite, expanding greatly at level of acropodite into short, broad hood overhanging and shielding latter, margins of hood irregularly serrate to jagged, with cavity on inner margin and many hairs arranged continuously along inner surface; females unknown.

*Color in life.* — Unknown. Though faded, the Florida male shows evidence of stripes along the caudal metatergal margins connecting with the paranotal markings and expanding in the midline; the collum is striped along both margins.

**Holotype.** — Body highly fragmented, length unmeasurable, maximum width 5.1 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Head partly decomposed, facial characters obtained from paratype.

Collum not extending below ends of following tergite. Paranota moderately depressed, partly continuing slope of dorsum; posterior corners rounded through segment 10, blunt on 11-12, becoming progressively more acute caudally.

5th sternum with short, narrowly segregated, knob-like processes between anterior (4th) legs and broader, higher, widely separated ones between 6th legs; 5th sternum with subsimilar knob-like projections between both leg pairs, those between caudal (7th) legs slightly higher. Postgonopodal sterna with strong, subconical, widely separated lobes subtending coxae of 9th legs, only slightly shorter than widths of latter; remaining sterna with short, broad lobes between both legs on segment 8, becoming progressively flatter posteriorly, with modest hair patches beside legs on all segments. 2nd coxa with strong subconical anterior, and slightly shorter posterior lobes. Prefemoral lobes extending through segment 15.

Gonopodal aperture (Fig. 142) ovoid, without caudolateral pouches, with strong anterior indentation, 2.1 mm wide and 1.1 mm long at maxima; anterior indentation relatively long, triangular, apically acute; sides not divided, angling slightly mediad, rising gradually and continuously to short lobe at caudolateral corner, rims smooth; caudolateral corner broad, indistinct; caudal margin continuous with lobe at caudolateral corner, dropping rapidly a short distance from latter to metazonal

surface, curving across midline and extending slightly caudad; margins irregularly hirsute with scattered hairs on anterior margin, none on indentation, relatively dense hairs arising on outer surfaces of sides and extending rather continuously to end of elevation on caudal margin, lobes without denser hairs. Gonopods *in situ* (Fig. 142) with bases of telopodites touching or nearly so in midline, diverging and extending well beyond caudal margin of aperture, overhanging 9th coxae, terminating over caudal margin of 7th segment, apices directed dorsad. Gonopod structure as follows (Figs. 142-145): Telopodite terminating at level of distal extremities of hairs. Prefemur very long, comprising entire length of telopodite, apically glabrous, configuration slightly curved with lengthy linear section in middle, apex bending more strongly dorsad, narrow basally, expanding markedly at midlength, narrowing slightly at distal bend, then expanding in perpendicular plane into short, broad, marginally serrated hood, inner surface strongly concave, with two rows of continuous, regularly spaced hairs on inner and lateral margins extending to just short of distal bend and level of acropodite, distomedial tuft of 6 or so hairs extending to midlength of hood, and one or two more proximal hairs medially. Acropodite a short, blunt spur on inner surface of prefemur, shielded ventrally but not surrounded by hood, directed outward or dorsad.

**Male paratype.** — Fragmented, unmeasurable. Width across genal apices 3.9 mm, interantennal isthmus 1.1 mm. Antennae reaching back beyond caudal margin of 3rd tergite, relative lengths of antennomeres  $2 > 6 > 4 > 5 > 3 > 1 > 7$ . Genae without impressions. Facial setae as follows: epicranial and interantennal absent, subantennal 1-1, frontal 1-1, genal 2-2, clypeal about 11-11, labral about 21-21. Process of mandibular stipes relatively long, angling slightly caudad, apically rounded (Fig. 141).

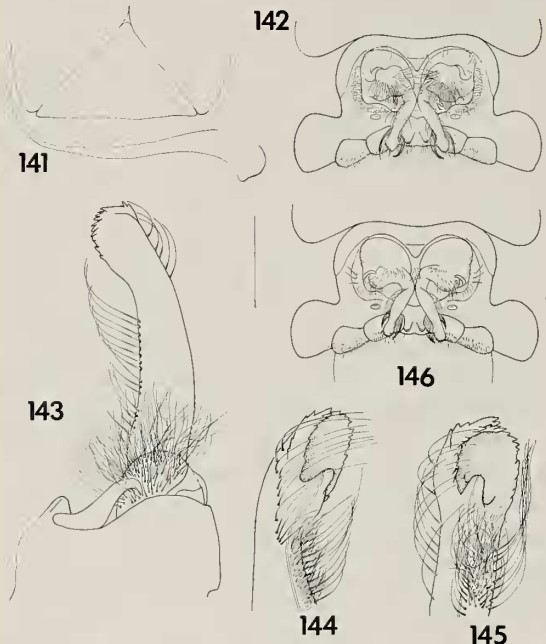
The male paratype agrees closely with the holotype, which is remarkable considering the 700 mile gap between them. The sternal projections on segments 4 and 5 are perhaps slightly longer, but otherwise there are no differences in somatic features. The aperture is considerably less hirsute, but its configuration is very similar to that of the holotype (Fig. 146). The elevations begin more suddenly a short distance back from the anterolateral corner, plateau, and continue around the caudolateral corner into a less distinct lobe, located more on the caudal margin. Aside from a slightly different degree of serration on the hood, the gonopods are virtually identical.

**Variation.** — The male from Little Rock agrees closely with the holotype in all particulars.

**Ecology.** — There are no indications of habitat on the vial labels with the Arkansas males. That from Florida was found on top of litter at the base of a small water oak in a wooded transition zone between slash pine and water oak.

**Distribution.** — Known from two widely separated sites, about 700 miles apart, in central Arkansas and northern Florida (Fig. 54). It is unknown whether these reflect truly allopatric populations or if the hiatus contains numerous additional populations, such that the range is reasonably continuous. Specimens were examined as follows:

ARKANSAS: *Pulaski Co.*, Cato, just S of Faulkner Co. line, M, 11 October 1955, Coffee (FSCA) TYPE LOCALITY; and Little Rock, M, 1880's, Hutcherson (NMNH).



Figs. 141-146. *Eurymerodesmus serratus*. 141, projection of right mandible of paratype, lateral view. 142, aperture and gonopods *in situ* of holotype, ventral view. 143, left gonopod of the same, lateral view. 144, telopodite of the same, medial view. 145, the same, dorsal view. 146, aperture and gonopods *in situ* of male from Alachua Co., FL, ventral view. Scale lines for figs. 142 and 146 = 1.00 mm. Line for other figs. = 0.25 mm for 141, 0.30 mm for 143, and 0.50 mm for 144-145.



FLORIDA: *Alachua Co.*, 10 mi. SE Gainesville, along FL hwy. 325, 4 mi. S jct. FL hwy. 20, M, 4 November 1978, G. B. Edwards (FSCA).

*Remarks.* — The three males of this species are so highly fragmented that length measurements would be meaningless. However, the animals can be characterized as “moderately-large,” i.e. smaller than such species as *goodi* and *dubius*, but larger than other intermediate-size species like *hispidipes*. The male from Little Rock is only a partial specimen, consisting of segments 6-9, and was mixed in the same vial with the neotype and two fragmented male variants of *pulaski*. Since this sample was labeled “*Leptodesmus hispidipes*” by Bollman in his handwriting, *serratus* probably constitutes part of the basis for his published record (1888a). Included in this vial is part of a female, which I characterized in the *pulaski* account but which may be referable to *serratus*. The bulk of the NMNH sample consists of mixed segments that cannot be segregated either by sex or species. The holotype and paratype were preserved intact, but they were so rigid and tightly coiled that they shattered when I tried to open them for examination, determination, and measurement.

The configuration of the telopodite of *serratus* is remarkably similar to those of the xystodesmids *Sigmoria* (*Cheiropus*) *planca* (Loomis) and *S. (C.) serrata* Shelley (see Shelley 1984b, figs. 3-7, 19-22) in being expanded distally into a marginally serrated hood, partly shielding the structure carrying the prostatic groove, the solenomerite in the species of *Sigmoria*. This is a remarkable example of convergence, and as in *S. (C.) serrata* the eurymerodesmid hood is actually quite jagged. The margin is thickened, particularly on the lateral side, and in places there are up to three rows or layers of sharp, tiny teeth that line the inner margin overhanging the cavity as well as the outer border. Seen in profile from the proper perspective, the apex of the telopodite of *serratus* closely resembles a mitten, with the acropodite being the thumb and the hood representing the other fingers combined, which was the basis for Loomis' name, *planca*. The jagged nature of the distal margin is by far the dominant feature, and except for the inner prefemoral margin of *crassatus*, no other eurymerodesmid is even slightly irregular. Smooth gonopodal margins are the rule in this family.

#### The *Birdi* Lineage

The *birdi* lineage is characterized by continuous, broadly terminal, and poorly demarcated acro-

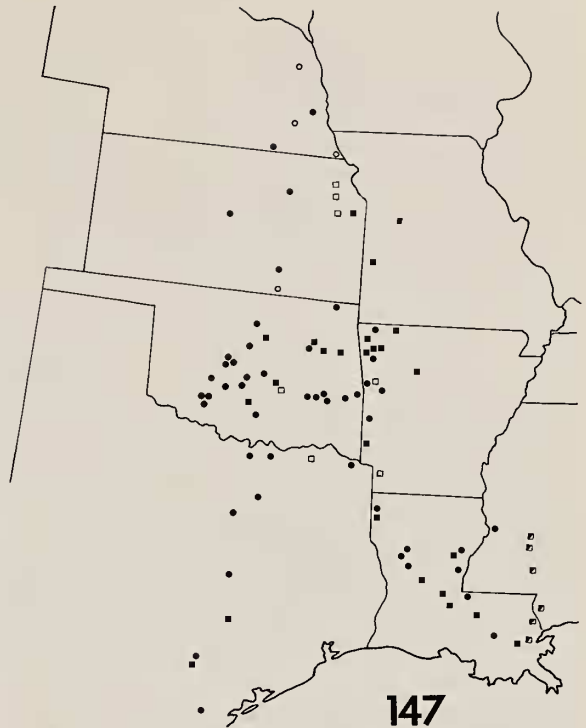


Fig. 147. Distribution of the *birdi* lineage. Squares, *birdi birdi*; half-shaded squares, *birdi planus*; dots, *mundus*. Open symbols denote literature records considered reliable.

podites; sides of apertures undivided, without caudolateral pouches; and caudal margins either with densely hirsute lobes or comparatively dense hair patches in this location. Females cannot be reliably distinguished from those in other groups. In lobed forms the densest marginal hairs are on the projections, so when the latter are absent, the densest patches are usually at this general location, suggesting that pilosity is the sole remaining remnant. Forms with lobes also display variably elevated lateral margins, which tend to be lower in ones lacking projections; the lobes arise from the elevations, and in general as one becomes smaller so does the other. In populations of *birdi planus* in southeastern Louisiana, there is only a low, continuous marginal elevation extending around the caudolateral corner without a trace of lobes, and in the northernmost population, the aperture is strikingly unadorned with only modest hair patches at the caudolateral corners. The sides and caudal margin of this form are either flush with the metazonum or so slightly elevated as to appear flat in ventral view.

The *birdi* lineage contains two forms with strong lobes, *mundus* and the western populations of *b. birdi*. The lobes are rigid, inflexible structures, and

here they are very large, extending ventrad well below the levels of the adjacent coxae, suggesting impairment of motility and promotion of ecological and/or behavioral adaptations. I have not encountered either species, but for clearance, it seems that the lobes must alter the animal's posture. If they do not carry themselves high off the substrate, the lobes would seemingly become embedded or broken. I saw no individuals with broken lobes nor any in which the apical hairs had been scraped off, indicating that the structures are unaffected by motion. Meaningful observations and ecological studies on these eurymerodesmids are desirable because of these prominent structural features.

The *birdi* lineage, comprised of a single species group, the *birdi* group, is the northernmost in the family, extending from northeastern Nebraska and central Mississippi to the Gulf Coast of Louisiana and south-central Texas (Figs. 147, 213-214). Its area ranks second in size to that of the *varius* group, *Kewanius* lineage, but it contains only two species instead of five.

*Components.* — *birdi* Chamberlin [*b. birdi*, *birdi planus* Causey], *mundus* Chamberlin.

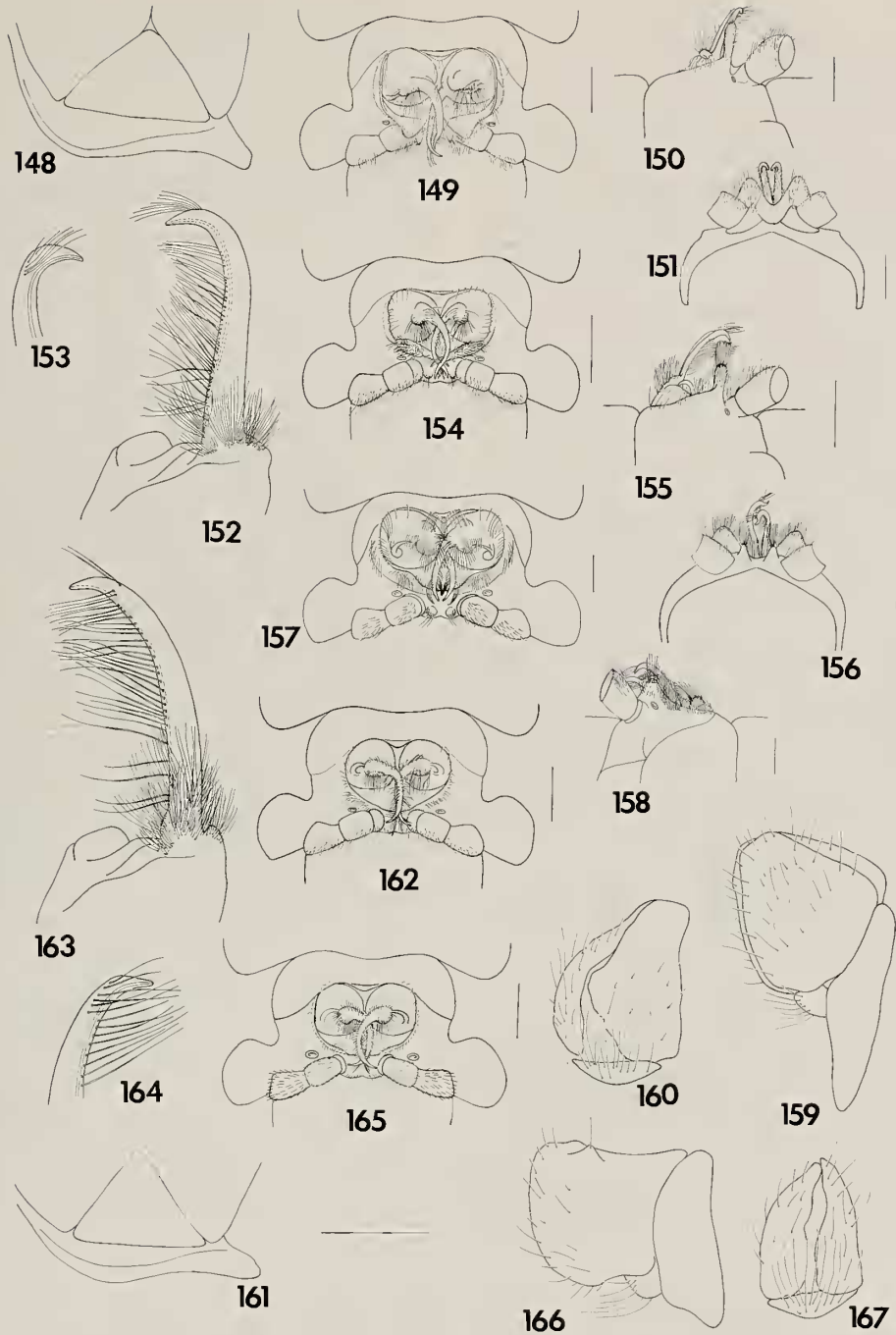
#### Eurymerodesmus birdi Chamberlin

*Diagnosis.* — A moderate-size species; males characterized by moderate to long mandibular projection; sides of aperture not divided, without caudolateral pouches, configuration variable, either flush with metazonal surface throughout, or elevating slightly, continuing around caudolateral corners, and descending a short distance along caudal margin, or elevating more strongly and continuing into variably long, broadly rounded, subtriangular lobes at caudolateral corners or on caudal margin; telopodite long; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners varying from slightly produced to elevated into short rim; receptacle large, sides not curved around operculum.

*Remarks.* — As represented by the types, the westernmost population of *birdi* possesses long aperture lobes that extend below the levels of the adjacent coxae. The projections are distinctive, easily recognized, and were adequately illustrated by Chamberlin (1931, fig. 8). This population occurs in Murray, Garvin, Seminole, and Pottawatomie counties, Oklahoma, and ones with equally long lobes occur sporadically to the east, for example in Vicks-

burg, Warren County, Mississippi. However, most forms outside these counties display variably shorter lobes, and there is a general trend toward smaller projections and lower marginal elevations as one proceeds southeastward in Louisiana. The lobes are also short north and south of these counties, but show no geographical trends. The projections disappear at New Orleans, leaving a low, uniform marginal elevation extending from the anterior halves of the sides around the caudolateral corners. In central Mississippi, the form named *planus* by Causey (1950b) exhibits an unadorned aperture without elevations but with modest hair patches at the caudolateral corners. The opening is flush with the metazonum, and the hair patches occur at the approximate position of the lobes. Southward towards New Orleans the sides and caudal margin begin to elevate, but always uniformly, without a trace of lobes. The evidence is not as convincing as in *varius*, where there is clear intergradation between *v. varius* and *v. christianus*, but I think that these forms with and without subtriangular lobes blend smoothly together, since forms in East Baton Rouge and West Feliciana parishes have very short lobes, barely detectable above the marginal elevations. Thus, *planus* is a form of *birdi*, the oldest name for this ensemble, and as first reviser, I assign *planus* to the populations lacking lobes, ranging essentially from New Orleans to near Jackson, Mississippi. The only other population showing reasonable anatomical stability is the one in central Oklahoma with large lobes represented by the types of *birdi*. However, if it is designated the nominate subspecies, the intergrade area will be vastly larger than that of either race, since the other three available names — *creolus*, *schmidtii*, and *plishneri* — apply to forms in areas of high instability. This solution is impractical, and I therefore combine all forms with detectable lobes under the nominate subspecies, essentially everything north and west of New Orleans, including a few localities east of the Mississippi River. In contrast to *varius*, I do not recognize an intergrade region *per se* in *birdi* because this is virtually the entire range between New Orleans and central Oklahoma. Consequently, *birdi* is the most intricate eurymerodesmid next to *amplus*, since it encompasses the second greatest array of variants. Causey (1950b) was amply justified in considering *planus* a valid species, for it could hardly be more distinct from the types of *birdi*. However, these forms are merely opposite ends of a complex spectrum of lobed eurymerodesmids that Chamberlin (1931) was the first to name.





Figs. 148-167. *Eurymerodesmus birdi*. 148, projections of right mandible of holotype, lateral view. 149, aperture and gonopods *in situ* of holotype, ventral view. 150, the same, lateral view. 151, the same, caudal view. 152, left gonopod of the same, lateral view. 153, telopodite of the same, medial view. 154, aperture and gonopods *in situ* of male from Caddo Par., LA, ventral view. 155, the same, lateral view. 156, the same, caudal view. 157, aperture and gonopods *in situ* of male from Polk Co., AR, ventral view. 158, the same, lateral view. 159, left cyphopod of allotype, caudal view. 160, the same, lateral view. 161-167, *birdi planus*. 161, projection of right mandible of holotype, lateral view. 162, aperture and gonopods *in situ* of holotype, ventral view. 163, left gonopods of the same, lateral view. 164, telopodite of the same, medial view. 165, aperture and gonopods *in situ* of male from Pearl River Co., MS, ventral view. 166, left cyphopod of female from Simpson Co., MS, caudal view. 167, the same, dorsal view. Scale lines for figs. 149-151, 154-158, 162, and 165 = 1.00 mm. Line for other figs. = 0.30 mm for 148 and 161; 0.40 mm for 152, 163, and 166-167; and 0.50 mm for 153, 159-160, and 164.

**Eurymerodesmus birdi birdi** Chamberlin, new status  
Figs. 147-160, 211-232

*Leptodesmus hispidipes*: Gunthorp, 1913:162 (in part). Chamberlin, 1918:370 (in part).

*Eurymerodesmus birdi* Chamberlin, 1931:101-102, figs. 6-8. Attems, 1938:185-186, figs. 204-205. Causey, 1952b:1-2. Chamberlin and Hoffman, 1958:79. Stewart, 1969:384.

*Eurymerodesmus creolus* Chamberlin, 1942a:6, pl. 2, fig. 16. Chamberlin and Hoffman, 1958:79. **NEW SYNONYMY.**

*Eurymerodesmus schmidtii* Chamberlin, 1943:38, fig. 7; 1952:573. Causey, 1952b:2. Chamberlin and Hoffman, 1958:81. **NEW SYNONYMY.**

*Eurymerodesmus plishneri* Causey, 1950a:271, fig. 8. **NEW SYNONYMY.**

*Type specimens.* — Male holotype, one male paratype, and female allotype (NMNH) collected by R. D. Bird, 17 October 1929, from an unknown site in Murray Co., OK.

*Diagnosis.* — Apertures with distinct subtriangular lobes of varying lengths at varying positions along caudal margin to caudolateral corners.

*Color in Life.* — Peritremata orange; metaterga gray-brown with orange stripes along caudal margins connecting paranotal markings; collum with stripes along both anterior and posterior margins (Causey 1950a). Causey further states that the metatergal stripes are usually wider mediad, rendering a trimaculate appearance resembling the syntopic platyrhacid *Auturus evides* (Bollman). Chamberlin (1931, 1942a, 1943) also recorded the striped pattern, but from faded preserved specimens.

*Holotype.* — Body highly fragmented, length unmeasurable, maximum width 4.2 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.7 mm, interantennal isthmus 0.7 mm. Antennae missing, length and relative lengths of antennomeres unknown, recorded from paratype. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, subantennal 1-1, frontal 1-1, clypeal about 8-8, labral about 13-13. Projection of mandibular stipes long, stout, bluntly rounded (Fig. 148).

Collum extending slightly below ends of following tergite. Paranota depressed, continuing slope of dorsum; posterior corners rounded through segment 8, blunt on 9-13, becoming progressively more acute posteriorly.

5th sternum with broad, flattened, paramedian processes between both leg pairs; 6th sternum with subconical processes between both coxae. Postgonopodal sterna with subconical projections between 9th legs; remaining sterna with shorter subconical lobes on segment 8, becoming progressively flatter posteriorly with variable bicruciform impressions and variable hair tufts subtending coxae, becoming sparser caudally. 2nd coxa with short, rounded anterior, and longer, subacuminate caudal lobes. Prefemoral lobes extending through segment 16.

Gonopodal aperture (Figs. 149-151) subrectangular, without caudolateral pouches, with moderate anterior indentation, 1.8 mm wide and 0.7 mm long at maxima; anterior indentation short, broad, rounded; sides entire, nearly linear, becoming progressively

more elevated caudad, leaning slightly over opening, rims essentially smooth; caudolateral corner broad, rounded; caudal margin continuous laterally with sides, extending immediately into enormous, broadly subtriangular lobe, leaning caudad, narrowly segregated in midline from opposite lobe and thus occupying nearly half of breadth of aperture, lobe extending well below margins of adjacent coxae, apex broad, rounded, perhaps 1/3 as wide as base, dropping to metazonal surface just before midline; margins irregularly hirsute with long hairs arising from rim or short distances down outer surfaces and overhanging opening, with several hairs on anterior indentation, scattered hairs on sides and caudolateral corner, hairs shorter and very dense on all surfaces of lobes, becoming slightly denser distad. Gonopods *in situ* (Fig. 149) with telopodites overlapping opposite member in midline, extending caudad between aperture lobes and terminating between 9th legs below level of apices of lobes. Gonopod structure as follows (Figs. 152-153): Telopodite terminating before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite length, linear for most of length, curving distad, sides parallel for most of length, tapering smoothly and continuously distad with two rows of continuous, regularly spaced hairs along inner margin and distomedial tuft of about six hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, continuing curvature of latter, sides tapering rapidly to acuminate tip.

*Male paratype.* — Body fragmented, length unmeasurable. Antennae reaching back to anterior half of 3rd metatergite, relative lengths of antennomeres 2 > 4 > 3 > 5 = 6 > 1 > 7. Somatic and gonopodal features closely similar to those of holotype.

*Female allotype.* — Length 22.2 mm, maximum width 3.6 mm, W/L ratio 16.2%. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal and frontal setal series absent. Projection of mandibular stipes short, blunt. Sterna relatively flat and unmodified, without projections, with only a few randomly scattered setae, especially along caudal margins.

Cyphopodal aperture subrectangular, caudal margin distinctly elevated above metazonal surface. Cyphopods *in situ* with valves oriented transversely, edges of valves and corner of receptacle visible in aperture, open side facing dorsad. Valves (Figs. 159-160) large, moderately hirsute, slightly unequal, anterior one larger, distal margins elevated into short rim. Receptacle large, glabrous, located laterad to valves, sides curving partly around operculum. Latter relatively large, located at bases of valves on dorsal side.

*Variation.* — Size varies markedly, with the smaller individuals occurring to the north in Missouri and Kansas and the largest specimens in Polk County, Arkansas. Elsewhere body proportions seem random and probably reflect habitat conditions. Piecing together males with no more than two fragments the following measurements were made:

Table 5. Size variation of *E. b. birdi* males.

State	County	Length (mm)	Width (mm)	W/L ratio (%)
Kansas	Douglas	22.0	3.4	15.5
Oklahoma	Payne	24.1	4.0	16.6
Oklahoma	Garvin	27.0	4.4	16.3
Arkansas	Washington	28.7	4.5	15.7
Arkansas	Polk	37.8	5.3	14.0
Louisiana	Natchitoches	33.9	5.0	14.7
Texas	Bowie	33.2	4.8	14.5



The gonopods are relatively constant throughout the range but the angle of projection from the aperture varies from nearly directly ventrad with the tips leaning slightly between the aperture lobes, to caudad, with the apices extending directly between and beyond the lobes, and overhanging the sternum between the 9th legs. On the apertures, considerable variation obtains in the configurations of the lateral margins, the size and degree of separation of the caudal lobes, and the hirsuteness of the lateral and caudal margins. Since the lobes are the most prominent feature, differences in their relative proportions are particularly noticeable, and I analyzed this geographically. The longest lobes occur primarily in forms along the western range periphery, around the type locality in central Oklahoma, where all males exhibit them. Elsewhere they are random. These lobes are moderately hirsute, much longer than the widths of the 9th coxae, usually extend ventrad below the telopodites, are relatively broad, and are narrowly segregated in the midline. Together they comprise most of the caudal margin of the aperture and are aligned with the sternal processes between the 9th legs (Fig. 151). Thus, a subspecies could be recognized from Seminole, Pottawatomie, Murray, and Garvin counties, Oklahoma, but elsewhere the lobes vary randomly and capriciously with too little stability, even within single populations as reflected by the larger samples, to justify taxonomic recognition. In the most common configuration (Figs. 154-156), the lobes are subequal to or only slightly longer than the 9th coxae, do not extend ventrad below the telopodites, and are more widely segregated thus being situated more laterad, at or partly on the caudolateral corners, and "outside" the succeeding sternal processes as seen in caudal profile (Fig. 156). However, this form intermingles sporadically with ones with shorter lobes located either more laterad or mediad (Figs. 157-158), and the male from Mississippi has long lobes like the form in central Oklahoma. In the male from East Baton Rouge Parish, Louisiana, the lobes are situated at the caudolateral corners and are so widely segregated that the caudal margin seems to lack them. A specimen from Grand Ecore, Natchitoches Parish, exhibits a uniformly elevated caudal margin without a trace of lobes, as in *b. planus*, but the other male in this sample has prominent lobes. Males from West Feliciana and Jefferson parishes show very small lobes, only slightly higher than the marginal elevations, and those in south Texas are small to moderate-size, with extremely long hairs in some individuals. Finally, the lobes are not always

equal in a single individual; in a few males, one is clearly longer than the other. Thus, aside from central Oklahoma, *b. birdi* does not exhibit a consistent set of features, thus obviating additional races. If future studies indicate otherwise, *creolus* has priority over both *schmidti* and *plishneri*.

Aside from the length and position of the lobes, they can also extend either directly ventrad or lean anteriorly or caudad, accordingly creating narrower or broader openings. Where they lean anteriorly, the aperture appears wider along the anterior margin. The degree of hirsuteness of the lobes and the lateral margins vary, and some males are exceptionally hairy with long, matted hairs, nearly as long as the lobes themselves, extending from their tips and anterior and caudal margins (Fig. 155). On the sides of the apertures, hairs arise mostly from the rim, but on sporadic individuals they also extend varying distances down the outer surface (Figs. 157-158). These lateral marginal hairs can also be very long, overhanging up to perhaps 1/4 of the width of the aperture.

The lateral elevations also vary, in many individuals arising smoothly and continuously beginning at the anterolateral corners and curving around the caudolateral corners into the lobes. In other males the elevations begin a short distance back of the anterolateral corners, producing a "stepped" effect in conjunction with the lobes. In some such individuals, the elevated parts of the lateral margins lean inward over the opening, causing it to appear wider along the anterior border.

*Ecology.* — The specimen reported by Chamberlin (1942a) was collected under a log in Caddo Parish, Louisiana; Causey (1950a) mentioned that oaks were dominant at the six recorded localities of *plishneri* in Washington and Carroll counties, Arkansas. The following habitat data was indicated on vial labels: on a driveway (Payne Co., OK); on a patio (Garvin Co., OK); under rocks in woods (Wagoner Co., OK); in an old stump, in rocks, and in water wells (Natchitoches Par., LA); under logs (Caddo Par., LA); in hardwoods at a lumber yard (West Feliciana Par., LA); and in sandy post oak soil (Wilson Co., TX). The milliped was collected in caves in Seminole, Cherokee, and LeFlore counties, Oklahoma, one of three eurymerodesmids known from subterranean habitats along with *oliphantus* and *melacis*. These areas are either on the western periphery of the Ozark and Ouachita Provinces or the eastern fringe of the Central Plains and may or may not represent accidental records.

*Distribution.* — From the southern Central Lowland Physiographic Province south of the Missouri River in northeastern Kansas and central Missouri, through the western Ozark Plateau and Ouachita Provinces to northeast Texas and the southern Mississippi Valley, with additional, possibly allopatric, populations in south-central Texas on the western fringe of the Coastal Plain (Figs. 147, 211-212). Specimens were examined as follows:

KANSAS: *Douglas Co.*, Lawrence, 3M, September 1977, R. Graham (RLH); and Univ. of Kansas Nat. Hist. Res., M, 2F, 29 September 1961, R. C. Funk (EIU) and 3M, 4 October 1966, D. Clark (FSCA). *Johnson Co.*, 3 mi. E. Eudora, M, 4 October 1966, D. Clark (FSCA).

MISSOURI: *Johnson Co.*, Knob Noster, 2M, 7F, 29 September 1962, and 11M, 25 F, November 1962, E. Peterman (FSCA). *Vernon Co.*, Nevada, M, 1 October 1961, D. J. McReynolds (MCZ).

OKLAHOMA: *Cherokee Co.*, 3 mi. SE Ft. Gibson Dam, Dressler Cave, 5M, F, 21 March 1971, J. H. Black (FSCA). *Wagoner Co.*, Lake Bixhoma, M, 1 March 1975, J. M. Nelson (NCSM). *Payne Co.*, Stillwater, M, 15 March 1984, R. M. Edwards (OKSU). *Pottawatomie Co.*, Dale, M, 3F, September 1954, Brown (FSCA). *Seminole Co.*, locality unknown, M, May 1931, P. Newport (SMUO); and Whiskey Cave, M, 6 January 1974, J. H. Black (FSCA). *Garvin Co.*, locality unknown, 4M, F, 2 November 1984, B. Lucas (OKSU). *Murray Co.*, locality unknown, 2M, F, 17 October 1929, R. D. Bird (NMNH) TYPE SPECIMENS, and 2M, F, 3 juvs., 17-26 October 1928, R. D. Bird (SMUO); Sulphur, M, 18 April 1976, W. Magdych (SMUO); and near Turner Falls, Arbuckle Mts., M, 23 April 1936, L. Hubricht (NMNH). *LeFlore Co.*, 10 mi. NE Talihina, Bear Den Cave, 4M, 17 November 1973, J. H. Black (FSCA).

ARKANSAS: *Benton Co.*, 5 mi. E Siloam, Chamber Spgs. Ranch, 3M, 2 September 1955, C. E. Hastings (FSCA); and Bella Vista, 2M, 13 April 1962, H. Hart (FSCA). *Carroll Co.*, Blue Springs, 3M, F, 29 October 1949, N. B. Causey (FSCA). *Washington Co.*, Springdale, Eden's Bluff, 3M, 8F, 2 juvs., 1 October 1949, N. B. Causey (FSCA); Fayetteville, M, 8 April 1959, N. B. Causey (FSCA), Mt. Kessler, M, F, 11 April 1949, N. B. Causey (ANSP) and 2M, F, 3 November 1949, collector unknown (FSCA), and Univ. of Arkansas campus, 2M, 10 February 1953, L. Jackson (FSCA); nr. Prairie Grove, Cove Cr. Valley, 18M, 23F, 4 juvs., 1 November 1955-25 March 1960, M. Hite (FSCA);

and Devil's Den St. Pk., M, 3F, 2 juvs., 29 September 1948, N. B. Causey (FSCA) and M, December 1963, N. B. Causey (MCZ). *Pope Co.*, locality unknown, M, 6 February 1955, B. Bowie (FSCA). *Logan Co.*, along AR hwy. 23 nr. Booneville, M, 19 November 1966, M. Hite (FSCA). *Polk Co.*, Rich Mtn., Mena, 11M, 2F, 21-22 March 1938, K. P. Schmidt (FMNH, NMNH), and 5M, 7F, 1950-May 1956, A. McWilliams and N. B. Causey (FSCA).

MISSISSIPPI: *Warren Co.*, Vicksburg, M, 7 February 1933, O. F. Cook (NMNH).

LOUISIANA: *Caddo Par.*, 5 mi. NW Shreveport, M, 13 April 1936, L. Hubricht (NMNH); and Shreveport, 3M, 9F, 3 juvs., 24 March 1962, N. B. Causey (FSCA). *Natchitoches Par.*, locality unknown, 25M, 13F, October 1954-February 1956, various collectors (FSCA); Natchitoches, Northwestern State Univ. campus, 7M, 12F, 3 juvs., February 1954-March 1956, J. E. Sublette and C. Morehead (FSCA); and 16 mi. SSE Natchitoches, 2M, 3F, 16 October 1965, D. E. Hahn (FSCA). *Rapides Par.*, along LA hwy. 28, 8.8 mi. E Gardner, 8M, 7F, 7 November 1965, R. E. Tandy and L. D. Wilson (FSCA). *Concordia par.*, Tensas R., 2M, 1954, B. Stanberry (FSCA). *Avoyelles Par.*, Evergreen, 2M, 4F, 28 October 1965, M. Kordisch (FSCA). *Evangeline Par.*, 2.5 mi. S Chicot St. Pk., M, 2F, juv., 30 January 1968, E. D. Kaiser (FSCA). *St. Landry Par.*, along LA hwy. 10, 2 mi. W Mellville, M, 3F, 24 March 1965, R. Tandy (FSCA). *East Baton Rouge Par.*, Louisiana St. Univ. Campus, M, November 1971, collector unknown (FSCA). *West Feliciana Par.*, locality unknown, M, F, 18 March 1962, L. Hubricht (RLH). *Jefferson Par.*, Narahan Jct., Elmwood Plantation along River Rd. at Research Dr., 0.3 mi W jct. US90, 2M, 2F, juv., 17 February 1986, R. M. Shelley (NCSM).

TEXAS: *Bowie Co.*, along US hwy. 259, 5 mi. S Red River, M, 9 December 1967, T. C. Stewart (SFAU). *Bell Co.*, Belton, M, January 1931, collector unknown (NMNH). *Bastrop Co.*, Bastrop St. Pk., 2M, 2 April 1960, J.C. Loomis (RLH). *Wilson Co.*, 8 mi. N Floresville, 2M, 29 April 1961, collector unknown (FSCA); and 8 mi. N Stockdale, M, 6 April 1961, J. F. Quinlan (FSCA). *San Patricio Co.*, Lake Corpus Christie St. Pk., M, 2 July 1969, J. R. Heitzman (FSCA).

The following literature records of additional localities are believed to refer to *b. birdi* and are so indicated in figures 147 and 211-212.

KANSAS (Gunthorp, 1913, cited as *Leptodesmus hispidipes*): *Jefferson Co.*, no further data.



OKLAHOMA (Causey 1952b); *Hughes Co.*, no further data.

ARKANSAS (Causey 1952b): *Sebastian Co.*, no further data. *Miller Co.*, no further data.

LOUISIANA (Chamberlin 1918, cited as *Lep-  
todesmus hispidipes*): *Natchitoches Par.*, Creton.

TEXAS (Stewart 1969): *Lamar Co.*, 8 mi. SE Paris.

Additional samples with a male from White Rock, Arkansas (FSCA), and a male and several females from Pacheco, Texas (FSCA), cannot be located in maps or gazetteers of these states.

*Remarks.* — The males from Norman, Cleveland County, Oklahoma (SMUO), which Chamberlin designated paratypes of *birdi* are actually specimens of *mundus*.

The label with the sample from 8 mi. N Floresville, Wilson Co., TX, states that the milliped was "very common, usually paired and grouped," but does not indicate whether the pairing was between opposite sexes.

The male from Payne County, Oklahoma (OKSU), has an accessory gonopod at the right anterior position of segment 8, the first example of heteromorphosis in the Eurymerodesmidae. The structure is shorter than normal and enclosed within a small circular aperture that does not extend across the midline. The lateral margin is normally elevated and extends into a typical caudal lobe, subequal in length to those on segment 7. A normal leg occurs opposite the accessory gonopod at the left anterior position of segment 8.

**Eurymerodesmus birdi planus** Causey, new status  
Figs. 147, 161-167, 211

*Eurymerodesmus planus* Causey, 1950b:196-197, fig. 5. Chamberlin and Hoffman, 1958:80.

*Type specimen.* — Male holotype (ANSP) collected by S. Bender, 13 April 1950, from Piney Woods, Rankin Co., MS. According to Causey (1950b) the type series also contained three females, now lost.

*Diagnosis.* — Apertures without lobes at any position, usually with denser hair patches at caudolateral corners, with or without uniform marginal elevations, arising on anterior halves of sides, curving around caudolateral corners, terminating before midline on caudal margin (Figs. 162, 165).

*Color in life.* — Paranota orange; metaterga dark with orange stripes along caudal margins connecting paranotal markings; collum with orange stripes

along both anterior and posterior margins (Causey 1950b). Causey also mentioned the presence of a roughly triangular median orange spot on some metatergites, perhaps reflecting expansion of the stripe in the midline, and several small, confluent orange dots on others. A paratype female had "two to six" orange dots on the metatergites.

*Variation.* — All specimens were tightly coiled and would not unroll without fragmenting into two or more pieces. A male from Pearl River County, Mississippi, which only broke into two pieces, measured approximately 24.0 mm long, 3.4 mm wide, W/L ratio 14.2%.

As stated, the holotype exhibits an unadorned aperture, margins being flush with the metazonum. Its only attributes are modest hair patches at the caudolateral corners, which really are nonexistent since the sides curve strongly mediad. Consequently, the aperture is proportionately the smallest in the genus and is heart-shaped in overall appearance (Fig. 162). The gonopods are a little more curved than the linear ones of the nominate subspecies (Figs. 163-164).

The Simpson County males from Braxton are near topotypes, occurring just across the county line from the type locality. Here the sides of the aperture are slightly but distinctly elevated beginning at the anterolateral corners. In the males from Jefferson Davis County, the caudolateral corner is angled and slightly more elevated; thus the caudal margin slopes downward from the corner, meeting the metazonal surface in the midline. Essentially the same condition obtains in the Pearl River County males (Fig. 165), except the caudolateral corner is rounded and leans over the aperture in one male. All Mississippi males exhibit hairs at the caudolateral corners, their densities and lengths varying, being longest in the last sample.

The Louisiana males display essentially the same conditions as those from southern Mississippi. In the St. Tammany Parish specimens, the moderately elevated sides continue around a squared caudolateral corner, then slope to the metazonal surface near the midline. In that from New Orleans, the sides are essentially flush with the metazonal surface, with the caudolateral corner being slightly elevated and rounded. The caudal margin extends slightly in the midline in all Louisiana males, and the hairs continue a short distance beyond the caudolateral corner in the New Orleans male.

The mandibular projection of the holotype is shorter and broader than in the nominate race (Fig.

161). The female genitalia are closely similar to those of *b. birdi* (Figs. 166-167).

*Ecology.* — The samples from Pearl River County Mississippi, were collected in "flood plain, water oaks." Those from 2.5 miles south of Prentiss, Jefferson Davis County, were retrieved from a pitfall trap on a hillside in pine woods.

*Distribution.* — The southern Gulf Coastal Plain of Mississippi and southeastern Louisiana, ranging from Jackson to New Orleans (Figs. 147, 211). Specimens were examined as follows:

MISSISSIPPI: *Rankin Co.*, Piney Woods, M, 13 April 1950, S. Bender (ANSP) TYPE LOCALITY. *Simpson Co.*, near Braxton, 2M, 5F, 4 juvs., 1 April 1958, S. Lazell (FSCA); and Mendenhall, M, 2 January 1960, L. Hubricht (RLH). *Jefferson Davis Co.*, 3 mi. SSW Prentiss, along White Sand Cr., 2M, 25 December 1959, L. Hubricht (RLH); and 2.5 mi. SW Prentiss, 4M, 27 February 1987, P. K. Lago (RLH). *Pearl River Co.*, 11 mi. E Bogaloussa, LA, 6M, 4F, 21 January 1965, N. B. Causey (FSCA).

LOUISIANA: *St. Tammany Par.*, Talisheek, along Talisheek Cr., 2M, 12 December 1965, L. D. Wilson (FSCA); and 1 mi. W Talisheek, 2M, 9 February 1939, collector unknown (NMNH). *Orleans Par.*, New Orleans, city park, M, 20 February 1950, collector unknown (FSCA).

### *Eurymerodesmus mundus* Chamberlin

Figs. 147, 168-175, 211-212

*Leptodesmus floridus*: Kenyon, 1893:16.

*Leptodesmus hispidipes*: Gunthorp, 1913:162 (in part).

*Eurymerodesmus mundus* Chamberlin, 1931:102-103, figs. 3-5.

Attems, 1938:186-187, fig. 206. Causey, 1952b:2. Chamberlin and Hoffman, 1958:80.

*Type specimens.* — Male holotype and male paratype (NMNH) collected by D. Zeigler, 26 February 1930, at University (Norman), Cleveland Co., OK. One male paratype (NMNH) collected by R. D. Bird, 5 April 1929, at an unknown site in Cleveland County.

*Diagnosis.* — A moderate-size species; males characterized by long mandibular projection; sides of aperture not divided, without caudolateral pouches, elevating slowly around caudolateral corners onto caudal margin, extending into very large clavate lobes; telopodite long; acropodite short, about 1/8 of acropodite length, broadly terminal, poorly demarcated from prefemur; latter with many hairs arranged continuously along inner surface; cyphopod valves of females with distal corners slightly produced; receptacle moderate size, sides curving around operculum.

*Color in Life.* — Paranota red; metaterga brown with concolorous stripes along posterior margins connecting paranotal markings; collum with brick red stripes along both anterior and posterior margins (Chamberlin 1931). All specimens available to me were preserved with faded colors, but many still showed clear evidence of this striped pattern.

*Holotype.* — Body fragmented, length unmeasurable, maximum width 4.1 mm.

Somatic features similar to those of *E. hispidipes*, with following exceptions:

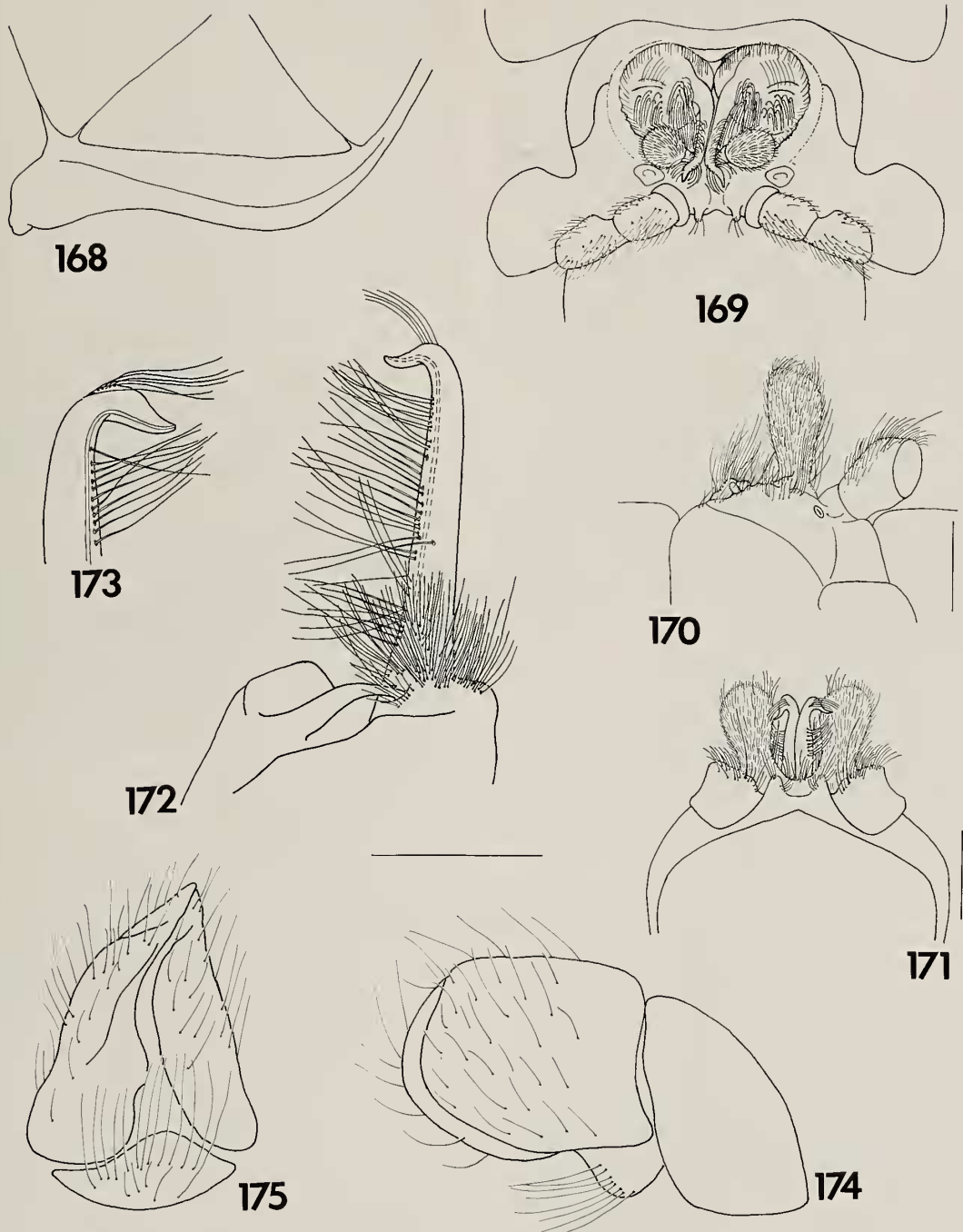
Width across genal apices 3.2 mm, interantennal isthmus 0.8 mm. Relative lengths of antennomeres 2>3>5>4>6>1>7. Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, frontal, and genal absent; clypeal about 11-11, labral about 14-14. Projection of mandibular stripes long and broad, ventral margin indented, tip smoothly irregular (Fig. 168).

Collum extending slightly below ends of following tergite. paranota moderately flattened, interrupting slope of dorsum; posterior corners rounded through segment 8, blunt on 9-14, becoming progressively more acute posteriorly.

5th sternum with short, widely separated knob-like processes adjacent to leg coxae; 6th sternum with broader, shorter, paramedial projections, caudal ones longer. Postgonopodal sterna with narrow, rounded, widely segregated lobes between 9th legs; remaining sterna with widely separated subconical lobes on segment 8 and flattened, elevated areas on 9, becoming progressively flatter posteriorly with variable transverse impressions between leg coxae, and shallow, faint to moderate central impressions rendering somewhat bicruciform appearance, all except 18th sterna with tufts of setae on ventral surfaces adjacent to leg coxae. 2nd coxa with large, rounded anterior, and narrower subconical posterior lobes. Prefemoral lobes extending through segment 16.

Gonopodal aperture (Figs. 169-171, not this specimen) ovoid, widest along anterior margin, without caudolateral pouches, with slight anterior indentation, 1.9 mm long and 0.8 mm wide at maxima; anterior indentation short, broadly rounded; sides curving mediad, not divided, rising slowly and progressively to caudolateral corner, rims slightly irregular; caudolateral corner indistinct, continuing curvature and rise of sides; caudal margin continuous through caudolateral corner with sides, lowly elevated for short distance then extending greatly ventrad into an enormous, clavate, lobe extending ventrad well beyond level of coxae, dropping to level of marginal elevation and curving across midline, lobes paramedian and narrowly segregated in midline, aligned just outside sternal processes between 9th legs; margins heavily hirsute with hairs arising regularly from rim and overhanging opening, thicker along anterior indentation, also arising from outer surfaces laterally and caudally, caudal lobes densely pilose, hairs beginning basally and becoming denser apically, hairs on lobes much shorter and denser than those from aperture rim. Gonopods *in situ* (Fig. 169, not this specimen) with telopodites touching or nearly so in midline, extending between, and terminating just beyond aperture lobes, apices directed sublateral. Gonopod structure as follows (Figs. 172-173): Telopodite terminating well before level of distal extremities of hairs. Prefemur long, about 7/8 of telopodite length, configuration linear, curving abruptly distad, sides parallel for most of length, tapering distad near level of curve, with two rows of continuous, regularly spaced hairs along inner margin culminating in slightly thicker tuft of six hairs, and distomedial tuft





Figs. 168-175. *Eurymerodesmus mundus*. 168, projection of left mandible of holotype, lateral view. 169, aperture and gonopods *in situ* of male from Comanche Co., OK, ventral view. 170, the same, lateral view. 171, the same, caudal view. 172, left gonopod of holotype, lateral view. 173, telopodite of the same, medial view. 174, left cyphopod of female from Canadian Co., OK, caudal view. 175, the same, dorsal view. Scale line for figs. 169-171 = 1.00 mm. Line for other figs. = 0.30 mm for 168, 0.40 mm for 172, and 0.50 mm for 173-175.

of about 6 hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, smoothly continuous with, and poorly demarcated from latter, bending sharply sublaterad, slightly bisinuate, sides tapering rapidly to acuminate tip.

*Male paratype.* — Agreeing closely with holotype in all particulars.

*Female from Canadian Co., OK.* — Length about 19.6 mm, maximum width 3.3 mm, W/L ratio 16.8%. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal setae 1-1, frontal setae 1-1. Mandibular stipes with minute rounded process. 3rd and 4th segments with moderate flanges lateral to legs. Sterna relatively flat and unmodified, without projections or tufts of setae.

Cyphopodal aperture subrectangular, caudal margin slightly elevated above metazonal surface. Cyphopods *in situ* with valves directed mediad, edges and side of receptacle visible in aperture, open side facing dorsad. Valves (Figs. 174-175) moderate-size, slightly unequal, anterior one larger and rounded, distal corners slightly produced. Receptacle moderately large, glabrous, located laterad to valves, sides curving partly around operculum. Latter relatively large, located at bases of valves on dorsal side.

*Variation.* — Size varies markedly, with larger specimens occurring in the center of the range from Oklahoma to Arkansas, and smaller ones occurring peripherally. Piecing together a few of the less fragmented males, with no more than two pieces, the following measurements were made. For most specimens merely straightening for measurement resulted in breakage.

Table 6. Size Variation of *E. mundus* Males.

State	County	Length (mm)	Width (mm)	W/L (%)
NE	Jefferson	21.9	3.2	14.6%
KS	Riley	22.4	2.9	12.9%
OK	Cleveland	31.1	5.0	16.1%
OK	Comanche	32.4	4.6	14.2%
AR	Sevier	33.9	5.6	16.5%
TX	Johnson	21.4	2.6	12.1%

The pregonopodal legs are more densely hirsute than those in the midbody region on some males, and in these individuals the legs become progressively less hirsute caudad. In some males the lateral margins of the gonopodal aperture are slightly excavated on the anterolateral corners. The distance between the caudal lobes varies, some being more widely segregated than others. In most individuals, the projections extend essentially directly ventrad, but in a few they diverge slightly laterad. These features occur randomly throughout the range. The lobes are virtually identical in length and configuration on all males except for the southernmost from Johnson County, Texas, where they are noticeably shorter and less clavate.

*Ecology.* — The holotype was collected in a "black jack forest" (Chamberlin 1931), presumably

blackjack oak litter, on or very near the University of Oklahoma campus. Vial labels with habitat notations are as follows: under a litter and under rocks in the Wichita Mountains (Comanche Co., OK), on the floor of a house (Tulsa Co., OK), under a log (Noble Co., OK), in a storm cellar (Grayson Co., TX), and under a rock in a pasture (Ellsworth Co., KS).

*Distribution.* — *Eurymerodesmus mundus* is the northernmost species with presumably reliable literature records from northeastern Nebraska and one with a voucher specimen from near Omaha. The known distribution covers the Central Lowland Physiographic Province from northeastern Nebraska to the Brazos River in northern Texas, extending eastward into the Ouachita and Coastal Plain Provinces in eastern Oklahoma and southwestern Arkansas (Figs. 147, 211-212). Neither *mundus* nor the family is known from north of the Missouri River. Discovery in western Missouri south of this watercourse is anticipated. Specimens were examined as follows:

NEBRASKA: *Cass Co.*, South Bend, 2M, date unknown, F. C. Kenyon (NMNH). *Jefferson Co.*, Reynolds, M, 7 October 1981, W. F. Rapp (MCZ) and M, 9 September 1987, W. F. Rapp (RLH).

KANSAS: *Riley Co.*, locality unknown, 2M, 2 April 1952, L. Warren (FSCA) and Manhattan, M, 2 May 1940, H. H. Walker (RLH). *Ellsworth Co.*, 6 mi. SW Ellsworth, M, 2 May 1976, C. L. Starr (UGA). *Butler Co.*, 8 mi. SE Augusta, M, 14 October 1935, Burt (NMNH).

OKLAHOMA: *Craig Co.*, 1 mi. S Kansas state line, F, 7 April 1973, J. H. Black (FSCA). *Tulsa Co.*, Bixby, M, 1 December 1980, J. M. Nelson (NCSM). *Noble Co.*, Perry, M, 11 May 1967, D. C. Arnold (WAS). *Logan Co.*, 5 mi. NE Guthrie, M, 28 October 1959, R. C. Harrel (FSCA). *Canadian Co.*, locality unknown, 5M, F, 1930, N. M. Newport (SMUO) and Yukon, M, 1930, N. M. Newport (SMUO). *Caddo Co.*, locality unknown, 3M, F, February 1934, Carpenter (SMUO). *Grady Co.*, Chickasha, F, 4 June 1944, L. Hook (FSCA). *Comanche CO.*, Wichita Mts., locality unknown, 2M, 16 October 1971, collector unknown (MSU), Mt. Scott, MM, FF, 25 October 1974, G. Beck (MSU); Sunset Rec. Area, 2M, 29 October 1977, J. C. Coken-dolpher and D. Parmley (MSU); Camp Boulder, F, 2 juvs., 8 June 1928, collector unknown (NMNH); and Panther Cr. Rec. Area, M, 6 November 1977, D. Parmley and K. Brice (MSU). *Cleveland Co.*, locality unknown, M, 5 April 1929, R. D. Bird (NMNH) and 2M, 20 February 1931, R. D. Bird (SMUO); and Norman, University, M, 10 March



1929, R. D. Bird (SMUO), M, 20 February 1937, D. Zeigler (NMNH) and M, March 1976, W. D. Butcher (SMUO) TYPE LOCALITY. *McClain Co.*, locality unknown, M, F, February 1933, Rosenmal (SMUO). *Pittsburg Co.*, McAlester, 2M, 2F, 10 February 1952, O. Murray (FSCA); and 3 mi. E Krebs, M, 2F, 22 October 1961, R. C. Harrel (FSCA). *Latimer Co.*, locality unknown, M, F, 25 April and 27 June 1931, R. D. Bird (SMUO) and 2M, F, 9 December 1933, Carpenter (SMUO); 5 mi. NW Wilburton, Robbers Cave St. Pk., M, F, 17 May 1960, R. C. Harrel (FSCA) and M, 25 October 1976, J. C. Cokendolpher (MSU); and Wilburton, M, 3F, 17 November 1934, Carpenter (ILNHS, SMUO). *LeFlore Co.*, 3.5 mi. N Howe, M, F, 26 May 1966, L. Hubricht (RLH).

ARKANSAS: *Polk Co.*, Rich Mt., Queen Wilhemina St. Pk., 2M, 8 November 1966, collector unknown (FSCA). *Sevier Co.*, Horatio, 4M, 8F, 11-15 April 1955 and 5 April 1956, C. N. Griffith (FSCA).

TEXAS: *Cooke Co.*, nr. old Townsite of Lea, M, 11F, 7 May 1968, collector unknown (FSCA). *Dallas Co.*, Dallas, 2M, 2F, June 1955, O. Sanders (FSCA); and between Duncanville and Cedar Hill, M, 3 November 1927, O. F. Cook (NMNH). *Johnson Co.*, Cleburne St. Pk., M, 26 December 1979, G. Spicer (NCSM).

The following additional literature records are believed to refer to *mundus* and are so indicated in figure 147.

NEBRASKA (Kenyon 1893, cited as *Leptodesmus floridus*, a synonym of *Semionellus placidus* (Wood) (Chamberlin and Hoffman 1958) ): *Cuming Co.*, West Point. *Lancaster Co.*, Roca. *Richardson Co.*, Rulo. *Unknown county*, La Platte.

KANSAS (Gunthorp 1913, cited as *Leptodesmus hispidipes*): *Cowley Co.*, no further data.

*Remarks.* — Labels in the holotype and paratype vials read "*Erymnogon*" *mundus* rather than *Eurymerodesmus*, indicating that Chamberlin originally thought this species required a new genus. The lobes probably created this impression, but he must have changed his mind, and fortunately "*Erymnogon*" was never validated, although it would have been available as a subgeneric designation for the *birdi* lineage. However, Chamberlin did incorrectly designate a male topotype in the SMUO as a paratype of *birdi*.

The sample from South Bend, Nebraska, collected by F. C. Kenyon, the northernmost known for the family, is identified as "*Leptodesmus floridus*." This was not among the Nebraska localities Kenyon

(1893) reported, but those he did — West Point, Rulo, Roca, and La Platte — probably also refer to *mundus*. Thus, I include his usage of *L. floridus* in the synonymy. The first three sites are indicated by open symbols in figure 147; the last is not on the official Nebraska map. Hence, the range for *mundus* probably extends north of the Platte River. I also include under *mundus* the Kansas records of *Leptodesmus hispidipes* by Gunthorp (1913), since they are either in or near the known range and likely refer to this species.

Chamberlin (1931) characterizes the lobes as arising from the sternum behind the gonopods, but his description of laminae extending ectad and cephalad from the structures implies that they are part of the aperture margin.

In addition to being the northernmost congener, *mundus* also forms the western boundary of the family in the northern part of the range (Fig. 147). The Missouri River seems to be a boundary, not only for *mundus* but also for the family. No eurymerodesmids have been taken to the north of this river in Iowa and northern Missouri. Consequently, I doubt if *mundus* occurs in the southeastern corner of South Dakota.

#### The *Melacis* Lineage

Located primarily in south and central Texas, on the known southern and western peripheries of the generic and family range, the *melacis* lineage is a nondescript assemblage with few distinguishing features. It is best characterized negatively, as the assemblage in Texas with short acropodites that lacks aperture lobes and pouches, and whose lateral margins are undivided. Common traits are small body size and short telopodites, which are either wholly enclosed by the aperture or just overlap the caudal margin, unless the specimen is exceptionally compressed. The apertures are comparatively small in three species, but *dactylocyphus* has proportionally the largest openings in the family. *Eurymerodesmus digitatus*, with intermediate-size openings, bridges the anatomical gap. Aperture margins are the most unmodified in the family; the sides are entire, and there are no lobes, pouches, or flares. Again *dactylocyphus* is an exception, with cupped, flange-like elevations at the caudolateral corners and adjoining parts of the sides and caudal margin, and again, *digitatus* spans the anatomical gap, at least in some populations. Although the telopodites are short, barely extending beyond the caudal aperture margin, the relative proportions of the prefemur and acropodite are as in the *birdi*

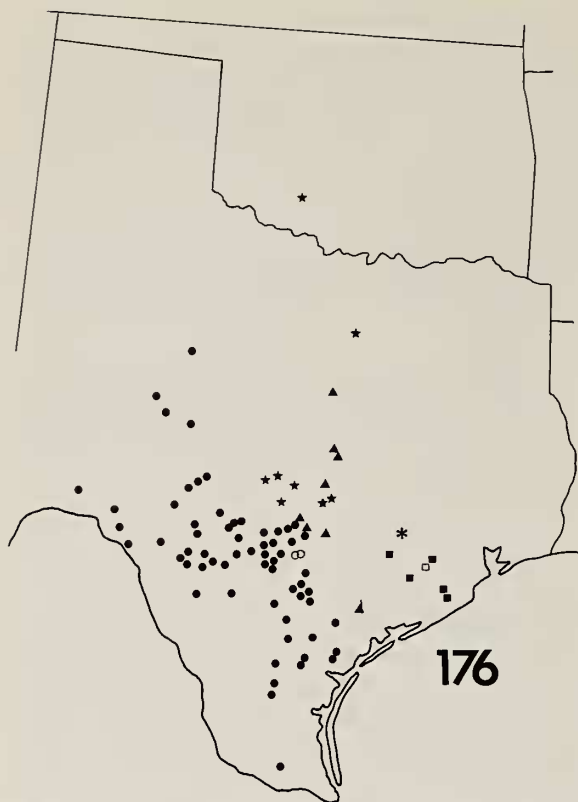


Fig. 176. Distribution of the *melacis* lineage. Dots, *melacis*; triangles, *dactylocyphus*; squares, *sanbernardiensis*; stars, *digitatus*; asterisk, *clavatus*. Open symbols denote literature records considered reliable.

lineage and *varius* group, with the prefemur constituting from 2/3 to 7/8 of the telopodite length. Acropodites are broadly terminal and continuous with the prefemur except for *clavatus*, where it is narrowly terminal, discontinuous, and sharply demarcated, arising from the outer prefemoral margin. This condition, accompanied by a clavate prefemur with a shoulder on the inner distal margin, is the obverse of that found in *simplex*, where the shoulder is on the outer surface, and the acropodite arises from the inner surface. Females do not display distinguishing features enabling them to be reliably identified, except again for *dactylocyphus* and to a lesser extent *digitatus*. The former possesses variable valvular projections ranging from small, nubbinlike papillae in eastern populations to long, flexible dactyliform structures in western forms that extend caudad and overhang two to three segments. This dactyliform condition is convergent with that in *compressus*, with the important distinction that the projections are flexible instead of being stiff and rigid. Thus the *melacis* group is characterized by small body size (all species); short telopodites (all

species); terminal, continuous acropodites (excepting *clavatus*); small, unadorned apertures (excepting *dactylocyphus*); and rather nondescript, unadorned cyphopod valves (excepting *dactylocyphus*).

Located in south Texas, south of and parapatric to most of the *varius* group, with an extension into southwestern Oklahoma, the *melacis* lineage is the only eurymerodesmid component that may extend into Mexico. Since it occurs practically to the north bank of the Rio Grande from Laredo to Del Rio, *melacis* itself may inhabit the northern fringes of Coahuila, Nuevo Leon, and/or Tamaulipas states in a manner similar to *Abacion texense* (Loomis) in the order Callipodida (Shelley 1984a). However, this watercourse could be a barrier, with a new species on the southern side. Since the family crosses several large US rivers, including the Mississippi, it may also traverse the Rio Grande, thereby occurring in northeastern Mexico and possibly farther south. Indeed, a new species group or lineage with several components may occur in Mexico, which may provide clues to the relationships of the family.

The *melacis* lineage is comprised of one species group, the *melacis* group, and five species.

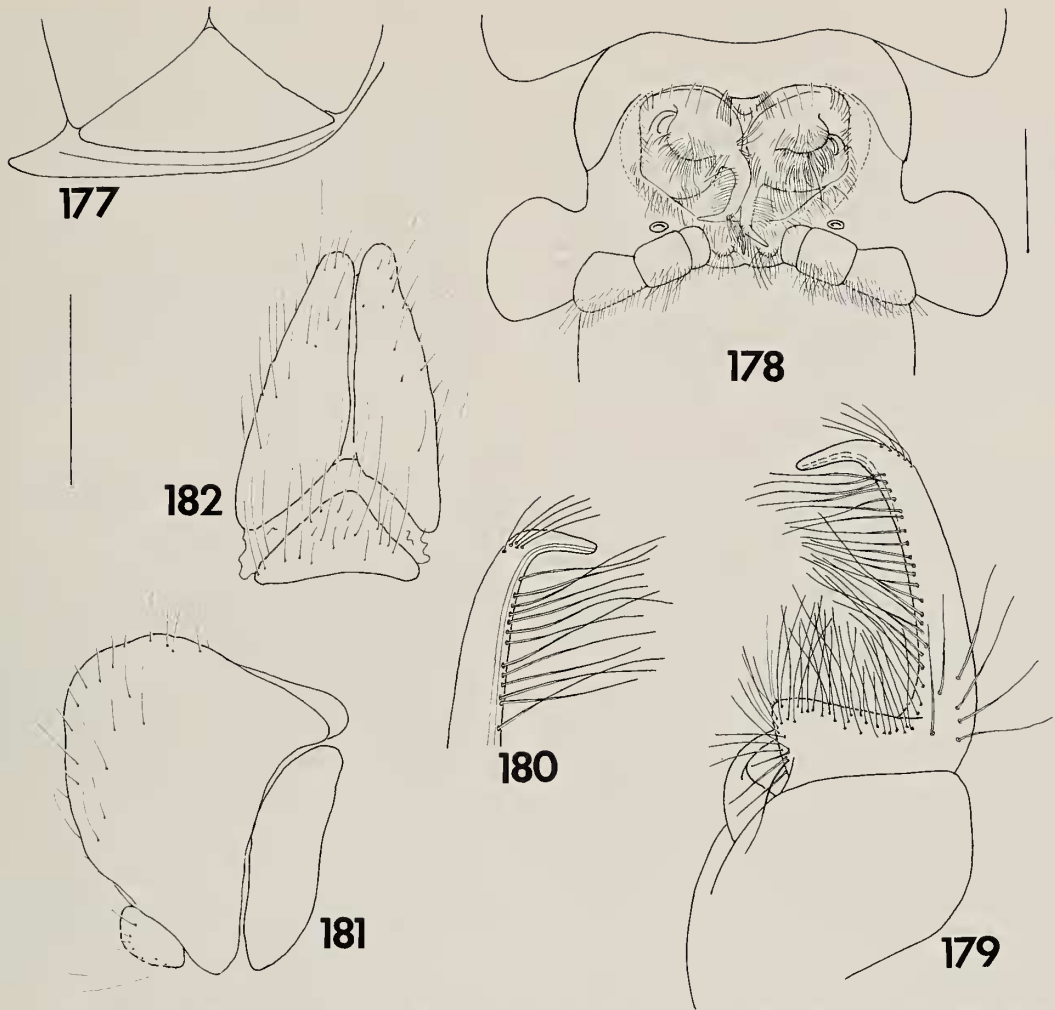
*Components.* — *melacis* Chamberlin and Mulaik; *sanbernardiensis* Causey; *digitatus* Loomis; *dactylocyphus*, new species; *clavatus*, new species.

#### *Eurymerodesmus melacis* Chamberlin and Mulaik Figs. 176-182, 212

*Eurymerodesmus melacis* Chamberlin and Mulaik, 1941:59-60.  
Chamberlin, 1952:573. Chamberlin and Hoffman, 1958:80.  
Loomis, 1959:161.

*Type specimens.* — Male holotype and 57 male, 20 female, and 12 juvenile paratypes (NMNH) collected by S. and D. Mulaik in December 1939 at Edinburg, Hidalgo Co., TX. Other paratypes, all taken by same collectors from localities in Texas and in the NMNH, as follows: Kerr Co., Raven Ranch, ca. 12 mi. S Kerrville, 4F, August 1939, and 22M, 2F, 3 juvs., December 1939; Kendall Co., locality unknown, 9M, 15F, December 1939, and Boerne, 6M, 2F, December 1939; and Bandera Co., locality unknown, 9M, F, December 1939, and 7 mi. N Medina, M, date unknown. The original description does not mention the holotype, and Chamberlin and Hoffman (1958) cited Raven Ranch, Kerr County, as the type locality. In the 11 vials of types, both a male from Edinburg and a female from Raven Ranch are labeled "holotype." Since the former is a male, I regard it as the holotype. A large series was taken from Edinburg at the same time as the





Figs. 177-182. *Eurymerodesmus melacis*. 177, projection of left mandible of holotype, lateral view. 178, aperture and gonopods *in situ* of paratype from Kerr Co., TX, ventral view. 179, left gonopod of holotype, lateral view. 180, telopodite of the same, medial view. 181, left cyphopod of female paratype from Hidalgo Co., TX, caudal view. 182, the same, medial view. Scale lines for fig. 178 = 1.00 mm. Line for other figs. = 0.25 mm for 177, and 0.50 mm for 179-182.

holotype, and the other specimens are properly considered paratypes. Chamberlin and Mulaik (1941) gave no reason for designating so many additional paratypes from other localities, which contrasts markedly with other species of *Eurymerodesmus* authored by Chamberlin where few paratypes were designated.

**Diagnosis.** — A small species; males characterized by moderate-size mandibular projection; aperture moderate-size, much narrower than ventral segmental width; sides not divided, without caudolateral pouches, with or without slight but continuous elevation with slight suggestion of lobe at caudolateral corners, descending to metazonal surface on caudal margin; telopodite short, usually only slightly overlapping caudal margin; acropodite,

short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, bending strongly laterad; prefemur with many hairs arranged continuously along inner surface; cyphopod valves of females not modified, distal corners not produced; receptacle moderate-size, sides not curving round operculum.

**Color in life.** — Peritremata brick red; dorsum black, metaterga with variably broad, brick red to orange stripes along caudal margins connecting concolorous peritrematal markings; collum with brick red to orange stripes along anterior and caudal margins. These are the colors I noted while collecting *melacis* in 1986. They correspond to Chamberlin and Mulaik's description (1941), who noted that the stripe expands along the midline.

*Holotype*. — Body highly fragmented, length unmeasurable, maximum width 3.2 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.4 mm, interantennal isthmus 0.8 mm. Antennae reaching back to just beyond 2nd tergite, relative lengths of antennomeres  $4 > 2 > 3 > 5 > 6 > 1 > 7$ . Genae with faint central impressions. Facial setae as follows: epicranial, interantennal, and genal absent, clypeal about 10-10, labral about 14-14. Process of mandibular stipes moderate-size, curving slightly inward, narrowly rounded apically (Fig. 177).

Collum extending slightly below ends of following tergite. Paranota depressed, continuing slope of dorsum; posterior corners rounded through segment 7, blunt on 8-12, becoming progressively more acute caudally.

5th sternum with low, rounded lobes between both leg pairs, caudal ones higher; 6th sternum with slightly longer lobes between anterior legs and strong, densely hirsute projections between 7th legs. Postgonopodal sterna with rounded, widely separated knobs between 9th legs; remaining sterna becoming progressively flatter and more plate-like caudally, with variable transverse grooves originating between leg pairs and hair patches adjacent to coxae, latter becoming progressively sparser caudally. 2nd coxa with minute anterior projection, caudal lobe absent. Prefemoral lobes extending through segment 15.

Gonopodal aperture (Fig. 178, not this specimen), broadly trapezoidal, without caudolateral pouches, with moderate-size anterior indentation, 1.6 mm wide and 0.8 mm long at maxima; anterior indentation broadly triangular, apically rounded; sides not divided, nearly straight, leaning slightly over opening, becoming slightly but progressively more elevated caudad, rims essentially smooth; caudolateral corner sharp, distinct, obtuse; caudal margin continuous with sides through caudolateral corner, angling strongly caudomedial, level for part of length with slight suggestion of rounded elevation, then tapering to metazonal surface and continuing flush with latter across midline; margins irregularly hirsute with long hairs arising from rim or short distance down outer surfaces of sides and overhanging opening, with tufts on sides of anterior indentation, lateral hairs becoming thicker caudally, densest on rounded part beyond caudolateral corner, diminishing medially. Gonopods *in situ* (Fig. 178, not this specimen) with telopodites crossing or overlying each other in midline, extending slightly beyond caudal margin of aperture and terminating above sternum between 8th legs, apices bent laterad. Gonopod structure as follows (Figs. 179-180): Telopodite short, terminating well before level of distal extremities of hairs. Prefemur proportionately long, about  $3/4$  of telopodite length, leaning slightly over coxa, with a continuous row of widely but regularly spaced hairs along inner surface and distomedial tuft of about 5 hairs. Acropodite short and broadly terminal, about  $1/4$  of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, bending strongly laterad, sides tapering continuously to blunt tip.

*Male paratypes*. — The male paratypes are all tightly coiled, and it is impossible to unroll and straighten most for measurement without breakage. Many shatter, rendering even length approximations impossible. The smaller specimens are more flexible and give the best measurements, but even they usually split between two pregonopodal segments. Approximate measurements on three specimens are length 22.5 mm long, 3.2 mm wide, W/L ratio 14.2%; 18.0 mm long, 3.5 mm wide, W/L ratio 19.4%; and 14.0 mm long, 2.1 mm wide, W/L ratio 1.50%.

The elevation of the sides of the Edinburg males varies, some being nearly flush with the metazonal surface. The caudolateral

corner varies, some being nearly flush with the metazonal surface. The caudolateral corner varies from obtuse to squared, or about a right angle, and the most significant differences concern the length of the elevation along the caudal margin and the abruptness of the slope to the metazonal surface. In a few males the elevation stops abruptly at the caudolateral corner, whereas it extends nearly to the midline with a long, gradual slope in others. The rim of the elevation is darkened in most males, and the opening extends significantly caudad in the midline in a few. In all specimens, the elevated part of the caudal margin is level with that of the sides, although males with longer elevations display a suggestion of a slightly higher rounded area just behind the caudolateral corners.

Paratypes from Kerr, Bandera, and Kendall counties closely resemble those from Edinburg. The sides are more linear in some and do not lean over the opening, and the rim is flared outward in a few.

*Female paratypes*. — An unbroken specimen from Edinburg measures 18.2 mm long, 3.0 mm maximum width, W/L ratio 16.5%. Agreeing essentially with males in somatic features, with following exceptions: interantennal setae 1-1, frontal 1-1. Mandibular stipes with minute projection, acuminate. Sterna flat and unmodified, glabrous.

Cyphopodal aperture elliptical, margins flush with metazonal surface. Cyphopods *in situ* with edges of valves visible in aperture, receptacle hidden under lateral margin. Valves (Figs. 181-182) oriented transversely in aperture, anterior valve slightly larger with rounded corner, moderate-size, extending dorsad on open side, distal margins not produced. Receptacle moderate-size, glabrous, located laterad to valves, sides not curving around operculum. Latter relatively large, clearly visible below open, dorsal, side of valves.

*Variation*. — *Eurymerodesmus melacis* is a brightly colored species with brick-red peritremata and metatergal stripes through most of the range and a mottled black base color. As noted by Chamberlin and Mulaik (1941) the stripes may be of uniform width or broader in the midline. In the western range periphery, colors assume more of an orange hue, becoming reddish-orange in Kinney County and orange in Tom Green County. The specimens I collected in the latter were so broadly striped and the pigment was so intense that they appeared entirely orange from a distance; actually the metaterga were almost entirely orange with the prozonum mottled black. Chamberlin and Mulaik (1941) described the antennae as pale with the ultimate and distal half of the penultimate articles black. I did not observe this pattern, and the antennae, as well as the genae and clypeus of the Kinney County specimens, were uniformly pale. These individuals exhibited mottled brown pigmentation on the frons, epicranium, and interantennal regions, as opposed to black on the segments, and the mandibular stipes were a lighter mottled brown. Chamberlin and Mulaik (1941) described the venter, sides, and legs as yellowish in the type specimens. The venter was white on the Kinney County individuals, and the legs possessed



brown flecks on the dorsal surfaces, extending onto the sides.

Because they were so tightly coiled and therefore broke or shattered with handling, measurements were impossible on most specimens of both sexes. A few recent molts had not fully hardened and were pliable.

Table 7. Size variation in *E. melacis*.

County	Males			Females		
	Length	Width	W/L	Length	Width	W/L
San Patricio	26.7	3.6	13.5%			
Terrell	17.1	2.6	15.2%			
Medina	25.1	3.7	14.7%	23.1	3.8	16.4%
Medina	21.2	3.0	14.1%	22.6	3.6	15.9%
Medina	21.8	3.3	15.1%	21.9	2.8	12.7%
Medina	23.2	3.8	16.4%	20.5	2.7	13.2%
Medina	21.8	2.9	14.3%	20.3	2.9	14.3%

Aperture variation is as discussed for paratypes. The telopodites appear slightly longer and narrower in scattered individuals, and the distances they extend caudad also vary depending upon how tightly the animal is coiled and how tightly the segments are compressed. In some the anterior half of the aperture is covered by the 6th segment. The lobes between the caudal legs on segment 6 are sharply conical in many individuals from Bexar and Jim Wells counties, being either subequal to or longer than the widths of the adjacent coxae. The process of the mandibular stipes is also quite broad in specimens from Karnes and Frio counties.

The Terrell County male, collected in a cave at the western periphery of the species and family, is by far the smallest adult male of *melacis* and the only one totally pallid, with no evidence of pigmentation. All other cave specimens show evidence of the striped color pattern even after years in preservative. The telopodites are also much shorter in this specimens and the acropodites are more linear and not bent as strongly laterad. Additionally, this male was flexible and easily unrolled for measurement; perhaps it is somewhat cave adapted.

The cyphopod valves are mostly uniform, being squared in profile with rounded corners. In the female from Helotes, Bexar County, the distal corners curve into short rounded lobes, and the corners are also slightly produced and rounded in one from Tom Green County.

*Ecology.* — In February 1986 *melacis* was common under small branches and shallow leaf layers in small oak thickets at the Welder Wildlife Refuge, San Patricio County. In Tom Green County, I found three specimens under large logs beside the

Concho River. Perhaps because of the unseasonable drought, I did not find *melacis* in the lush and ostensibly desirable bottomland forests along the Rio Grande in Cameron and Hidalgo counties, but it may be a desertine species actually preferring arid conditions. Thus, these forests may be unsuitable for *melacis*, but it should occur away from this habitat in drier, "inland" areas of Cameron, Hidalgo, and other south Texas counties. Notations on labels with preserved samples are as follows: under rocks (Frio, Kerr, and Uvalde cos.), under cow dung (Bee and Live Oak cos.), under logs (Wilson and Atascosa cos.), and under cardboard in "barditch" (Zavala Co.).

*Eurymerodesmus melacis* has been taken from 11 caves and can probably be anticipated in any cave in the range, where they are accidental inhabitants found primarily in the open on silt in entrance areas. Except for the specimens from Longley Cave, Terrell county, none vary significantly from epigeal populations. As suggested by the anatomical differences, these specimens may be true troglobites, since the opening to this cave is situated so as to virtually preclude the accidental entrance of epigeal forms (J. Reddell, pers. comm.).

*Distribution.* — The Gulf Coastal Plain and eastern Edwards Plateau of central and southern Texas as far west as eastern Terrell County, extending northward from the Rio Grande along the Gulf of Mexico to about the San Antonio River, and inland as far north as southern Hays and western Taylor counties (Fig. 176). Collections are concentrated along an arc running from Corpus Christi to San Antonio to Del Rio, and *melacis* appears rare in south Texas, perhaps an artifact reflecting sampling along major highways before the interstate era. Thus, I shade or outline all of south Texas in figures 1 and 213-214. Specimens were examined as follows:

TEXAS: *Taylor Co.*, 25 mi. SW Abilene, M, March 1944, H. S. Dybas (FMNH). *Tom Green Co.*, 17 mi. NW San Angelo, Wardlaw Ranch, M, F, 26 April 1967 and F, 27 November 1967, G. Brown (FSCA); and San Angelo, along Rio Concho, 2M, F, 27 February 1986, R. M. Shelley (NCSM). *Concho Co.*, 10 mi. W Eden, F, 15 December 1939, collector unknown (NMNH). *Kimble Co.*, Junction, M, 8 March 1986, R. W. Sites (NCSM); 4 mi. SW Junction, M, 24 March 1978, O. F. Francke, T. B. Hall, J. V. Moody (NCSM); and 13 mi. SW Junction, M, 2F, 24 March 1978, O. F. Francke, T. B. Hall, and J. V. Moody (NCSM). *Terrell Co.*, Longley Cave W of Pandale (Val Verde Co.), M, F, 27 June 1963, J. Reddell (FSCA). *Val Verde Co.*,

near Elliott Spider Cv., 8 mi. N Comstock, Marshall Ranch, M, 1 January 1965, J. Reddell (FSCA); and Del Rio, F, 9 October 1932, O. F. Cook (FSCA). *Edwards Co.*, 11 mi. NE Rock Springs, M, 24 March 1978, O. F. Francke, T. B. Hall, and J. V. Moody (NCSM). *Kinney Co.*, 21 mi. N Brackettville, 6M, 12 January 1985, S. A. Stockwell and J. M. Steller (NCSM). *Real Co.*, 13 mi. N Leakey, M, 23 March 1978, O. F. Francke, T. B. Hall, and J. V. Moody (NCSM); and Rio Frio, Prade Ranch, M, F, 21 April 1962, R. O. Albert (FSCA). *Uvalde Co.*, 26 mi. NW Uvalde, F, 12 September 1940, S. and D. Mulaik (NMNH); Laguna, 2M, 25 December 1941, collector unknown (AMNH); 12 mi. NW Uvalde, 5M, F, 23 March 1978, O. F. Francke, T. B. Hall, and J. V. Moody (NCSM); Knippa, M, F, 7 April 1937, K. P. Schmidt (FMNH); Sabinal, 2M, 2F, 4 juvs., 11 January 1933, H. C. McNamara (FSCA); Secret Valley Cv., exact location unknown, M, February 1984, R. M. Waters (NCSM); Tampke Ranch Cv., 0.8 mi. NE Uvalde, 2M, 11 February 1966, J. Reddell and D. McKenzie (FSCA); and Cedar Brake Cv., 25 mi. NE Uvalde, M, 25 October 1965, J. Reddell (FSCA). *Zavala Co.*, 1 mi. E Batesville, 16M, F, 15 March 1982, J. C. Cokendolpher (FSCA). *Kerr Co.*, Raven Ranch, ca. 12 mi. S Kerrville, off TX hwy. 173 north of Camp Verde, 4F, August 1939, 25M, 2F, 3 juvs., December 1939; 4F, juv. June-August 1940; and juv., June 1941, all by S. and D. Mulaik (NMNH); 14 mi. S Kerrville, 4M, 2F, 9 October 1976. J. C. Cokendolpher (MSU); and Seven Room Cv., 8 mi. SW Kerrville, 2 juvs., January 1966, J. Fish and J. Reddell (FSCA). *Bandera Co.*, locality unknown, 9M, F, December 1939, S. and D. Mulaik (NMNH); 7 mi. N Medina, M, date unknown, S. and D. Mulaik (NMNH); and Bandera, Shaw Ranch, 4M, 2 February 1962, G. Marion (FSCA). *Medina Co.*, 3 mi. ENE Mico, F, 19 March, year unknown, V. Roth (NCSM); D'Hanis, 13M, 16F, 3 juvs., 18 October 1932, O. F. Cook (NMNH); Windmill Cv., exact location unknown, M, 10 November 1984, S. J. Hardin and J. L. Ivy (NCSM); Koch Cv., 9 mi. N Hondo, M, 7 October 1963, J. Reddell and D. McKenzie (FSCA); and Boehme's Cv., exact location unknown, 19 December 1984, J. L. Ivy (TMM). *Frio Co.*, Pearsall, 2M, 4 February 1961, D. R. Whitehead (RLH). *Kendall Co.*, locality unknown, 9M, 15F, December 1939, S. and D. Mulaik (NMNH); and Boerne, 2M, 3F, 9 April 1911, W. P. Carr (NMNH) and 6M, 2F, December 1939, S. and D. Mulaik (NMNH). *Hays Co.*, Fern Bank Springs nr. Wimberly, F, 1 April 1961, R. Highton (RLH); San Marcos, F, 22 April 1941, K. P. Schmidt (FMNH); and Swift's Cv., exact location unknown, 26 June 1982, D. L. Pate (TMM). *Comal Co.*, between Startzville and Tom Cr., ca. 12 mi. NW New Braunfels, 2F, 15 March 1983, C. S. Lieb (NCSM); Brehmmer Cv., ca. 5 mi. W New Braunfels, F, 19 March 1960, W. J. Gertsch (AMNH); and New Braunfels, F, juv., 29 November 1942, E. S. Ross (CAS), M, 18 December 1954, L. Hubricht (RLH), and Landa Park, 4F, 19 June 1964, N. B. Causey (FSCA); and 2 mi. N Bergheim, 2M, 22 February 1986, S. J. Hardin (TMM). *Bexar Co.*, 20 mi. N San Antonio, 5M, 5F, 13 December 1942, E. S. Ross (CAS); Helotes, F, 6 April 1966, D. A. Rossman (FSCA); San Antonio, 2M, F, September, day, year, and collector unknown (MCZ), M, March 1925, A. H. Welolet (NMNH), Yturri Est., 15M, 10F, December 1905, O. F. Cook (NMNH), San Antonio R. at Roosevelt Ave., 16M, 12F, 23 October 1954, L. Hubricht (RLH), and Jessamine St., 11M, 3F, 31 October 1959, J. C. Loomis (RLH); 6 mi. S San Antonio, 4M, 2F, 7 December 1965, T. Stewart (FSCA); Camp Bullis, 15 mi. NW San Antonio, 2M, F, 27 January 1952, H. R. Bullock (AMNH) and 2M, F, 24 April 1966, B. Russell and D. McKenzie (FSCA); Black Cat Cv., 15 mi. NNE San Antonio, M, 2 December 1984, S. J. Harden and J. L. Ivy (NCSM); and Intermittant Spgs. nr. Leon Spgs., F, 3 November 1986, S. J. Harden and C. Lindblom (TMM). *Wilson Co.*, 4 mi. SE Poth, along Marcelinas Cr., M, 2F, 1 April 1961, J. F. Quinlan (FSCA); and 3 mi. W Falls City (in Karnes Co.), F, date and collector unknown (FSCA). *Atascosa Co.*, Campbellton, M, FF, 15 May 1961, J. F. Quinlan (FSCA). *Karnes Co.*, 1 mi. NW Falls City, M, 3F, 9 April 1961, J. F. Quinlan (FSCA); Falls City, M, F, 29 October 1961, J. F. Quinlan (FSCA); and Karnes City, 2M, 4F, 14 November 1959, N. B. Causey (FSCA). *Goliad Co.*, Goliad St. Pk., 3F, 17 April 1955, L. Hubricht (RLH). *Bee Co.*, Beeville, F, 11 November 1895, collector unknown (NMNH) and M, 28 December 1941, R. Perita (AMNH). *Live Oak Co.*, Largato, 2M, 2F, 18 February 1961, R. O. Albert (FSCA); 6 mi. SE Whitsett, 3M, 11 December 1984, R. S. Zack (WASU); and George West, 2M, 6F, 3 December 1960, collector unknown (FSCA). *Refugio Co.*, along Aransas R., F, May 1952, collector unknown (FSCA). *San Patricio Co.*, 7 mi. N Sinton, Welder Wildlife Ref., 40M, 26F, 8 juvs., February and December 1961, December 1965, and November 1970, R. O. Albert (FSCA), F, 18 October 1967, C. Parrish (CAS), and 8M, 5 juvs., 21 February 1986, R. M. Shelley (NCSM); and 4-5 mi. SW Mathis, 9M,



9F, 3 juvs., March 1961 and January 1962, R. O. Albert (FSCA). *Jim Wells Co.*, along Nueces R., 10M, 6F, 1-3 April 1962, R. O. Albert (FSCA). *Duval Co.*, unknown locality in NE corner, 2M, 2F, 4 April 1962, R. O. Albert (FSCA); San Diego, 9M, F, 8 January 1961, R. O. Albert (FSCA); and 5 mi. S San Diego, M, 2F, 17 February 1961, R. O. Albert (FSCA). *Hidalgo Co.*, Edinburg, 57M, 21F, 12 juvs., December 1939, S. and D. Mulaik (NMNH) TYPE LOCALITY.

Additional literature records for *melacis* deemed valid include McQueeney and Schertz, Guadalupe County (Loomis 1959).

*Remarks.* — Hoffman (1981) noted that some published Edinburg spider records are patently mislabeled, and since that for *melacis* is around 100 miles south of the closest known locality, in Duval County, the question as to whether it too may be erroneous assumes considerable importance, since Edinburg is now the type locality. The aforementioned absence of *melacis* from the forests of the Rio Grande Valley in contrast to its abundance in small thickets in San Patricio County is not troubling because *melacis* does not seem to be a forest-inhabiting species. The site where I collected it along the Rio Concho in San Angelo, Tom Green County, was grassland with a few widely scattered trees and no leaf litter, which I think reflects its habitat preferences. Since Edinburg is away from these woodlands, it is an ecologically plausible site for *melacis*. That no specimens have been collected in other counties in the tip of Texas, particularly intervening ones like Brooks and Jim Hoff, I think reflects their relative isolation. There are few towns or places to look for millipeds, and collectors passing through may have set their sights on the Rio Grande forests instead of the arid grasslands away from the river. Edinburg is not so far removed from other known sites as to be implausible, and there could also be an allopatric population there analogous to those of *b. birdi* in San Patricio, Wilson, Bastrop, and Bell counties. Thus, although confirmation with fresh material is desirable, Edinburg is a logical site for *melacis*.

As the southernmost species known essentially to the Rio Grande in Webb, Kinney, and Val Verde counties, *melacis* may be analogous to *Abacion texense* and occur south of the border in northern parts of Tamaulipas, Nuevo Leon, and/or Coahuila provinces, Mexico (Shelley 1984a). Mexican and American biologists working in these areas should be alert for this small, bright red millipede.

*Eurymerodesmus melacis* is also the westernmost

eurymerodesmid, and its occurrence on the eastern Edwards Plateau in central Texas suggests occurrence farther west in the Davis Mountains, the Permian Basin, the panhandle around Lubbock, and possibly even the southeastern corner of New Mexico. I therefore spent a week in February 1986 searching for it around Lubbock and in the Davis Mountains, with no success. I searched habitats similar to those in which I found it at San Angelo and the Welder Wildlife Refuge, but the only millipeds encountered were parajulids. Future discoveries are always possible, but I think the current western limits are close to the actual ones.

### *Eurymerodesmus dactylocyphus*, new species

Figs. 177, 183-189, 212

*Type specimens.* — Male holotype and two male and three female paratypes (FSCA) collected by R. O. Albert, 1 December 1963, at Maxwell, Caldwell Co., TX. One male and one female paratypes deposited in NCSM.

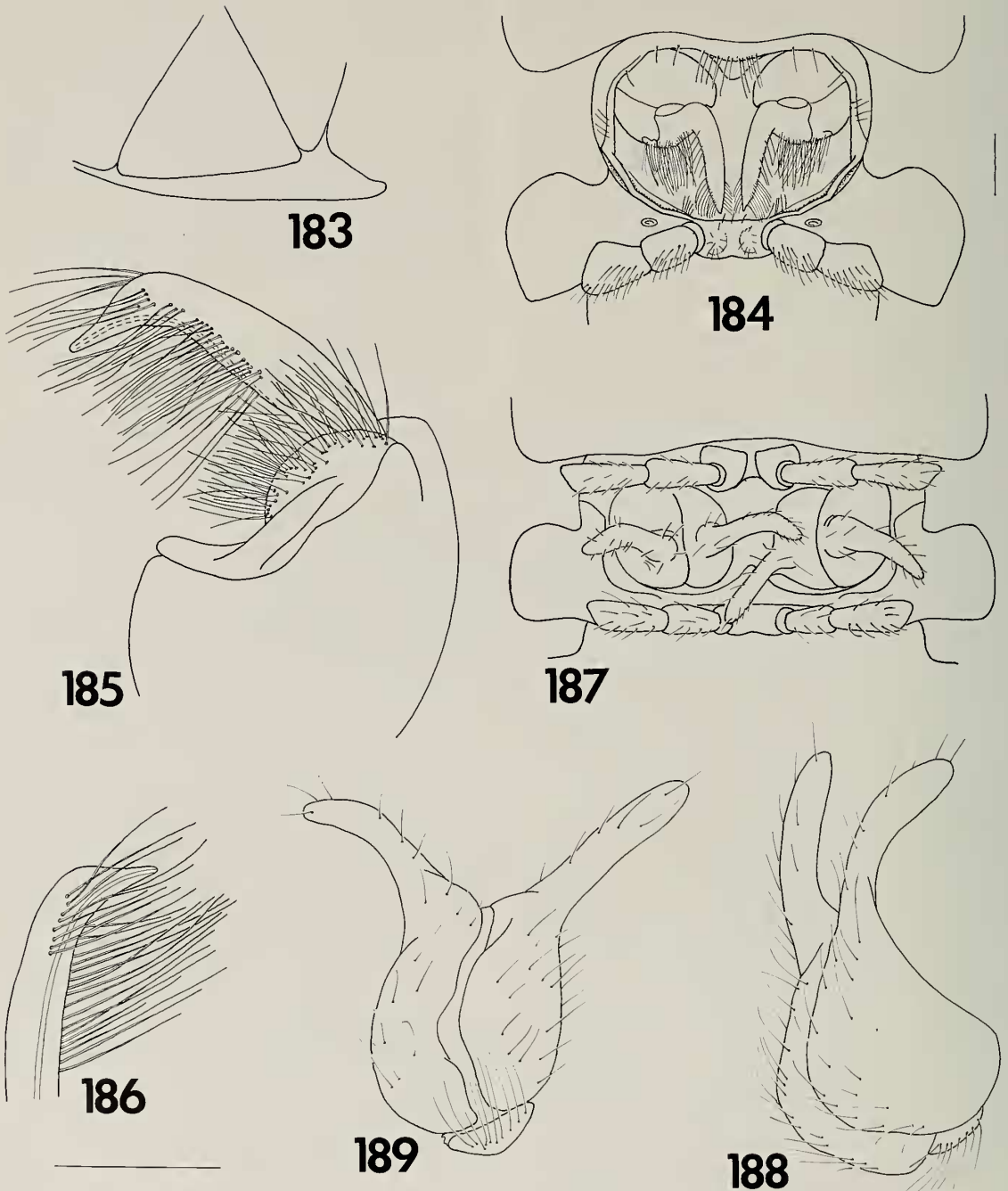
*Diagnosis.* — A small to moderate-size species; males characterized by long mandibular projection; aperture very large, occupying entire breadth of segment in ventral view; sides not divided, without caudolateral pouches, with variable caudal elevation continuing around caudolateral corners ranging from slight rise to long flange; caudal margin descending rapidly to metazonal surface; telopodite short, wholly enclosed within aperture; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, bending directly dorsad; cyphopod valves of females with distal corners of valves produced into variable projections, ranging from small nubbinlike tubercles to long, flexible dactyliform projections, extending well beyond cypopodal aperture and overlapping succeeding two segments *in situ*; receptacle small, submerged in valves, sides not curving around operculum.

*Color in Life.* — Unknown.

*Holotype.* — Length 19.7 mm, maximum width 3.0 mm, W/L Ratio 15.2%.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 1.8 mm, interantennal isthmus 0.6 mm. Antennae reaching back to caudal margin of 2nd tergite, relative lengths of antennomeres 2>3>6>4>5>1>7. Genae without impressions. Facial setae as follows: epicranial, interantennal, and genal absent, subantennal 1-1, frontal 1-1, clypeal about 10-10, labral about 14-14. Process of mandibular stipes relatively long, subtriangular, narrowly rounded apically (Fig. 183).



Figs. 183-189. *Eurymerodesmus dactylocyphus*. 183, projection of right mandible of holotype, lateral view. 184, aperture and gonopods *in situ* of holotype, ventral view. 185, left gonopod of the same, lateral view. 186, telopodite of the same, medial view. 187, cyphopods *in situ*, ventral view of female paratype. 188, left cyphopod of the same, medial view. 189, the same, anterior view. Scale lines for figs. 184 and 187 = 1.00 mm. Line for other figs. = 0.30 mm for 183 and 188-189, and 0.50 mm for 185-186.



Collum extending slightly below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, peritremata somewhat flattened; posterior corners rounded through segment 9, blunt on 10-12, becoming progressively more acute posteriorly.

5th sternum with small paramedian lobes between leg pairs; 6th sternum with broader, higher elevated areas. Postgonopodal sterna with low paramedian knobs between 9th legs; remaining sterna becoming progressively flatter, more plate-like, and less hirsute caudally, with variably distinct transverse grooves between pairs and broad central depressions, hairs diminishing after segment 9. 2nd coxa with large, rounded anterior and posterior lobes. Prefemoral lobes extending through segment 10.

Gonopodal aperture (Fig. 184) very large, nearly circular but broadly ovoid, without caudolateral pouches, with strong anterior indentation, 1.9 mm wide and 1.0 mm long at maxima, extending nearly to anterior edge of segment; anterior margin slightly elevated, in form of narrow rim continuing around anterolateral corners onto sides, anterior indentation broad, apically rounded; sides not divided, indented slightly and elevated at anterolateral corner, then linear for short distance, caudal half angling mediad, anterior half continuous with elevated anterior margin, elevation increasing rapidly and dramatically just beyond midlength, extending into long, broad, ventrally directed flange at caudolateral corners, rims mostly smooth, becoming slightly irregular on flange; caudolateral corners slightly angular, greatly elevated; caudal margin continuous with caudal elevation of sides, flange narrow, inner surface curved or cupulate, very long, extending nearly to midlength of podomeres, terminating abruptly a short distance beyond corner, margin low medially, curving across midline and merging with lobes between 9th legs; margins irregularly hirsute, with tufts of three to four hairs on anterior indentation, scattered hairs on rim of anterolateral corners and sides, a few arising from inner surfaces of flanges, and three to four on low, central part of caudal margin. Gonopods *in situ* (Fig. 184) with telopodites extending nearly directly caudad, angling slightly mediad, terminating short of caudal margin, wholly enclosed by aperture, apices directed dorsad. Gonopod structure as follows (Figs. 185-186): Telopodite relatively short, terminating well before level of distal extremities of hairs. Prefemur proportionally long, about 3/4 of telopodite length, leaning over coxa, broad basally, tapering slightly distad, with three rows of continuous, dense, regularly spaced hairs along inner margin and distomedial tuft of 8 hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, continuing distal curvature of latter, curving dorsad, sides narrowing rapidly to subacuminate tip.

*Male paratypes.* — The male paratypes agree with the holotype in all particulars.

*Female paratype.* — Length 22.1 mm, maximum width 2.8 mm, W/L ratio 12.7%. Agreeing essentially with males in somatic features, with following exceptions: Mandibular stipes with corner slightly produced, blunt. Sterna flat and unmodified, glabrous.

Cyphopodal aperture large, rectangular, caudal margin slightly elevated above metazonal surface, indented slightly anteriorly in midline. Cyphopods *in situ* (Fig. 187) with valves oriented along body axis, protruding slightly through opening, dactyliform projections extending well beyond aperture and overlapping legs of segments 3 and 4, directed either ventrad or laterad, appearing like supernumerary legs. Valves (Figs. 188-189) large, unequal, lateral one larger, distal corners extending into long, flexible, widely separated dactyliform projections, subequal to or longer than valves proper, projecting directly ventrad basally, curving caudad

at midlength, apically blunt. Receptacle small and inconspicuous, located on caudal side of, and submerged in, valves. Operculum small, located under anterior corner of valves.

*Variation.* — As described for the holotype, males from Hays County exhibit large, cupped aperture flanges, which drop nearly perpendicularly to the metazonal surface on the caudal margin just beyond the caudolateral corner. However, in Bell, Bosque, and Victoria counties the elevation is only slightly higher than the metazonal surface. The paramedian sternal projections between the 9th legs, very large and coalesced in the Victoria males, are subequal to the widths of the adjacent coxae, which have hirsute ventrodorsal lobes. In Bell County, the 9th sternal knobs are separate. On the gonopods, the prefemur tapers distad in the Hays County males and possesses a slight shoulder on the outer margin; thus, the acropodite is more strongly demarcated from the prefemur. In Bell County, the acropodite curves strongly dorsad.

The longest dactyliform cyphopodal projections occur in females from Hays and Caldwell counties. They are shorter, more variable, and more unequal in those from Bosque and Victoria counties. In the latter, the projections vary from small nubbinlike tubercles or papillae to digitiform elongations about half as long as the valves. Both conditions can occur on a single cyphopod.

*Ecology.* — Some of the Victoria specimens were encountered in sedge-grass roots in a sandy region and on a shaded river bank. A male from Bell County was collected along a fence.

*Distribution.* — The eastern fringe of the Central Plains to the Gulf of Mexico between the Brazos and Guadalupe Rivers (Figs. 176, 212). Specimens were examined as follows:

TEXAS: *Bosque Co.*, Meridian St. Pk., 5M, 26 December 1979, G. Spicer (NCSM) and 2M, 2F, 5 October 1980, G. Spicer (NCSM). *Bell Co.*, Belton, M, January 1931, collector unknown (NMNH); and 1 mi. W Belton, 2M, 24 December 1939 and 1941, collector unknown (AMNH). *Williamson Co.*, Three Mile Cv., ca. 3 mi. W Round Rock, M, 1 December 1962, R. O. Albert (TMM). *Hays Co.*, Fern Bank Springs nr. Wimberly, 2M, 1 April 1961, R. Highton (RLH); and San Marcos, F, 22 April 1941, K. P. Schmidt (FMNH). *Caldwell Co.*, Maxwell, 4M, 4F, 1 December 1963, R. O. Albert (FSCA) TYPE LOCALITY. *Victoria Co.*, Victoria, 50 M, 35 F, 7 juvs., December 1905, August 1906, 23 November 1911, 24 November 1912, 10 March 1913, and 11 December 1915, J. D. Mitchell (NMNH).

*Remarks.* — A female of *melacis* was found in the samples from Wimberly and San Marcos, suggesting that their ranges abut in southern Hays County. The male from Belton was retrieved from a sample of *b. birdi*, suggesting that the two species are sympatric in Bell County.

The gonopods of *dactylocyphus* appear ridiculously small in contrast to the enormous aperture. In some males the coxa is tucked under the anterior margin and appears swallowed by the aperture, which is mostly empty and thus filled with debris. The species has by far the broadest aperture in the genus, filling essentially the breadth of the metazonum in ventral view and extending laterad nearly to the level of the paranota. In some males, it compresses the prozonum into a remnant, an extremely narrow sliver, along the anterior segmental margin, the minimum necessary to give form to the aperture and hold it together. This is a striking feature of males, but I found the cyphopod projections equally sensational and decided to name the species for this distinctive aspect of females. These projections vary greatly, as described above, and the long ones are convergent with those in *compressus*. However, the projections in *dactylocyphus* differ in being flexible, as opposed to stiff and rigid. The projections are foreshortened in figure 187, appearing shorter than they really are, fully as long as the next two segments combined. In some females they project outward between the appendages of the following segment, thus appearing at first glance as additional legs, when seen in lateral view.

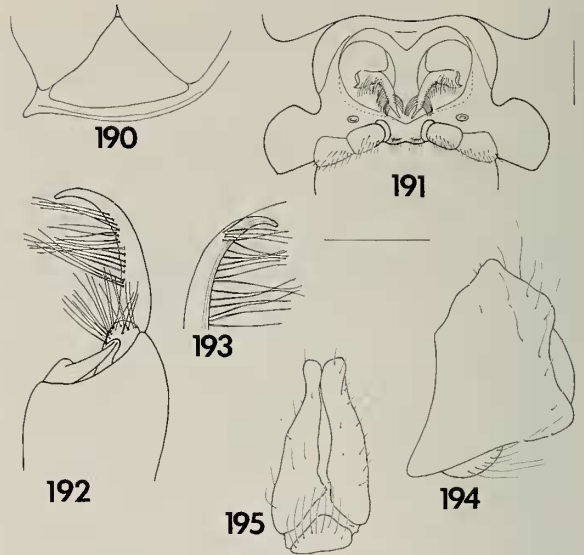
#### *Eurymerodesmus sanbernardiensis* Causey

Figs. 176, 190-195, 212

*Eurymerodesmus sanbernardiensis* Causey, 1952a:174, figs. 6-7. Chamberlin and Hoffman, 1958:81.

*Type specimen.* — Female holotype (ANSP) collected by N. B. Causey, 3 January 1952, along the San Bernard River near the crossing of US highway 59, Fort Bend Co., TX. The cyphopods and segment 3 are missing from the holotype and their separate vial at the ANSP, and are lost. My attempt to collect topotypes in February 1986 was unsuccessful. Since its cyphopods roughly resemble those in Causey's illustrations (1952a, figs. 6-7), I assign *sanbernardiensis* to the form occurring at Wharton, Wharton County, approximately 12 miles south of the type locality.

*Diagnosis.* — A small to moderate-size species; males characterized by short, triangular mandibular projection; aperture moderate-size, much narrower



Figs. 190-195. *Eurymerodesmus sanbernardiensis*. 190, projection of left mandible of male from Colorado Co., TX, lateral view. 191, aperture and gonopods *in situ* of the same, ventral view. 192, left gonopod of the same, lateral view. 193, telopodite of the same, medial view. 194, left cyphopod of female from Colorado Co., lateral view. 195, the same, anterolateral view. Scale line for fig. 191 = 1.00 mm. Line for other figs. = 0.40 mm for 190 and 195, and 0.50 mm for 192-194.

than ventral segmental width; sides not divided, without caudolateral pouches, elevating slightly around caudolateral corner, descending to metazonal surface along caudal margin; telopodite short, at most barely overlapping caudal margin of aperture; acropodite short, about 1/4 of telopodite length, broadly terminal, poorly demarcated from prefemur, curving broadly dorsad; prefemur with many hairs arranged continuously along inner margin; cyphopod valves of females with distal corners produced and rounded; receptacle small, partly submerged in valves, sides not curving around operculum.

*Color in life.* — Paranota orange; rest of color unknown. Causey (1952a) stated that the dorsum was mottled with orange, but that the color was "not completely developed."

*Male from Wharton Co.* — Length 22.7 mm, maximum 3.1 mm, W/L ratio 13.7%.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 1.8 mm, interantennal isthmus 0.8 mm. Antennae reaching back to midlength of 3rd tergite, relative lengths of antennomeres 2 > 3 > 4 > 6 > 5 > 1 > 7. Genae without impressions. Facial setae as follows: epicranial, interantennal, genal, and frontal absent, clypeal about 11-11, labral about 15-15. Projection of mandibular stipes short, triangular (Fig. 190).



Collum extending slightly below ends of following tergite. Paranota moderately depressed, mostly continuing slope of dorsum; posterior corners rounded through segment 8, blunt on 9-13, becoming progressively more acute posteriorly.

5th and 6th sterna with hirsute elevated areas between leg pairs, without lobes. Postgonopodal sterna flattened, plate-like, with variably complete transverse grooves originating between leg pairs on all segments and variably broad central depressions, with hair patches adjacent to leg coxae becoming sparser caudally. 2nd coxa with minute anterior swelling, without caudal lobe or swelling. Prefemoral lobes terminating on 12th legs.

Gonopodal aperture (Fig. 191, not this specimen) broadly ovoid, without caudolateral pouches, with broad anterior indentation, 1.2 mm wide and 0.8 mm long at maxima; anterior indentation moderately long, broadly triangular, apically acuminate; sides curving broadly, undivided, not leaning over opening, anterior half flush with metazonal surface, elevating at midlength and becoming slightly and progressively higher to caudolateral corner, rims essentially smooth; caudolateral corner obtuse, indistinct; caudal margin continuous with sides at caudolateral corner, tapering gradually to metazonal surface, extending slightly caudad in midline; margins glabrous. Gonopods *in situ* (Fig. 191, not this specimen) with telopodites angling caudomedial, terminating before level of caudal aperture margin, apices directed dorsad. Gonopod structure as follows (Figs. 192-193): Telopodite short, terminating well before level of distal extremities of hairs. Prefemur proportionally long, about 3/4 of telopodite length, curving over coxa, curve increasing distad, moderately broad basally, sides tapering distad, with two rows of continuous, regularly spaced hairs on inner surface and distomedial tuft of 5-6 hairs. Acropodite short and broadly terminal, about 1/4 of telopodite length, smoothly continuous with, and poorly demarcated from prefemur, continuing broad dorsal curvature of prefemur, sides tapering to subacuminate tip.

*Female from Wharton Co.* — Length 21.9 mm, maximum width 2.9 mm, W/L ratio 13.2%. Agreeing closely with males in somatic features, with following exceptions: frontal setae 1-1, genal 4-4. Mandibular stipes with short, rounded projection. Sterna flat and unmodified, glabrous.

Cyphopodal aperture elliptical, caudal margin slightly elevated above metazonal surface, indented slightly anteriorly at midline. Cyphopods *in situ* with valves oriented obliquely, distal corner protruding through opening. Valves (Figs. 194-195) small, unequal, caudal valve slightly larger, distal corners slightly produced and rounded. Receptacle small, inconspicuous, partly submerged in valves, located below latter on lateral side. Operculum small, located at bases of valves on medial side.

*Variation.* — The sides of the aperture are a little higher on two of the four males from Wharton County. Depending upon how submerged the coxae are in the aperture, the telopodites may or may not extend beyond the caudal margin and overhang the sternum between the 9th legs *in situ*. Specimens from Brazoria and Colorado counties agree closely with those from Wharton except for a slight bisinuate curvature on the acropodites of those from Colorado County. In these males the structure resembles a tarsal claw, since it is moderately long, similarly curved, and arises from a hirsute prefemur. Females are closely similar throughout the range.

*Ecology.* — The type locality, which I visited in February 1986 in an unsuccessful search for topotypes, is a narrow bottomland forest that merges into grassland a short distance away from the river. There were plenty of logs, debris, and other potential milliped habitat, but no eurymerodesmids. The female that I collected at Richmond, Fort Bend County, was found under leaves at a rest area near the Brazos River.

*Distribution.* — A small area of the Gulf Coastal Plain of southeastern Texas between the Brazos and Colorado Rivers, extending from the Gulf of Mexico to about 94 miles inland (Figs. 176, 212). Specimens were examined as follows:

TEXAS: *Austin Co.*, New Ulm, 9M, 6F, 3 February 1963, R. O. Albert (FSCA). *Colorado Co.*, Columbus, 3M, 23 December 1961, C. L. Redus (FSCA). *Fort Bend Co.*, ca. 2 mi. S Kendleton, along US hwy. 59 at San Bernard R., F, 3 January 1952, N. B. Causey (ANSP) TYPE LOCALITY; and Richmond, F, 20 February 1986, R. M. Shelley (NCSM). *Wharton Co.*, Wharton, Bank of Colorado R., 4M, 10F, 4 juvs., December 1905, collector unknown (NMNH). *Brazoria Co.*, Old Ocean and 2.4 mi. S Old Ocean, 2M, juv., 23 December 1961, R. O. Albert (FSCA).

*Remarks.* — In his key to Texas species of *Eurymerodesmus*, Loomis (1976) stated that the valves of female cyphopods of *sanbernardiensis* are of unequal length. This was probably based on Causey's description (1952a), which I think may have been of an immature female as judged by the size of the holotype versus Wharton females. As redefined here, the valves of *sanbernardiensis* are so nearly equivalent in size that this feature would not distinguish it from Texas congeners.

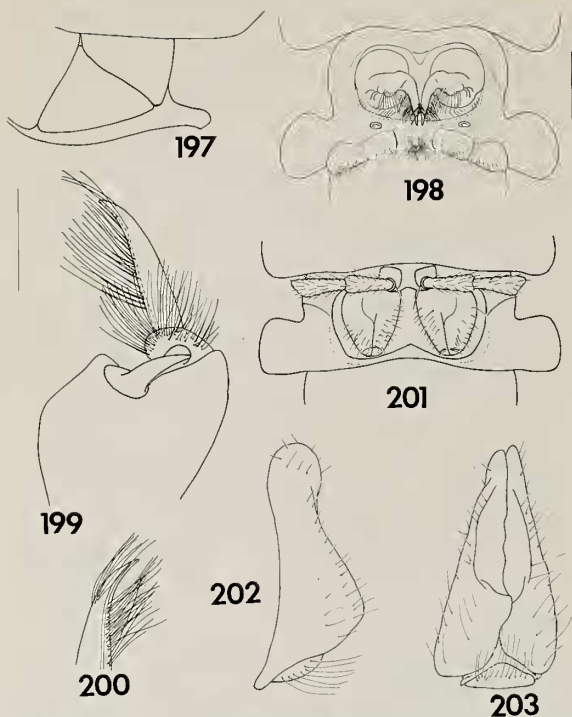
### *Eurymerodesmus digitatus* Loomis

Figs. 176, 197-203

*Eurymerodesmus digitatus* Loomis, 1976:288-289, figs. 1-3.

*Type specimens.* — Male holotype and female allotype (FSCA), and one male and one juvenile paratype (NMNH), collected by J. C. Loomis, 15 February 1975, 5 mi. ESE Marble Falls, Burnet Co., TX.

*Diagnosis.* — A small to moderate-size species; males characterized by long mandibular projection; aperture moderate-size, much narrower than ventral segmental width; sides not divided, without caudolateral pouches, elevating to various heights around caudolateral corner, descending to metazonal surface at varying distances along caudal



Figs. 197-203. *Eurymerodesmus digitatus*. 197, projection of right mandible of holotype, lateral view. 198, aperture and gonopods *in situ* of paratype, ventral view. 199, left gonopod of the same, lateral view. 200, telopodite of the same, medial view. 201, cyphopods *in situ*, ventral view of female from Llano Co., TX. 202, left cyphopod of allotype, oblique caudal view. 203, the same, oblique anterior view. Scale lines for figs. 198 and 201 = 1.00 mm. Line for other figs. = 0.35 for 1987, 0.40 mm for 202-203, and 0.50 mm for 199-200.

margin; telopodite usually short, usually barely overlapping caudal margin of aperture; acropodite short, about 1/8 of telopodite length, broadly terminal, poorly demarcated from prefemur, curving variably dorsad; prefemur with many hairs arranged continuously along inner margin; cyphopod valves of females usually with distal corners extended, broadly curved; receptacle small, indistinct, submerged in valves, sides not curving around operculum.

**Color in Life.** — Not known with certainty. Loomis (1976) reported that both the color and pattern were "apparently much as in *melacis*," but did not describe them *per se*. Thus, *digitatus* probably exhibits red paranota, red caudal metatergal stripes, and red borders on the collum.

**Holotype.** — Specimen highly fragmented, length unmeasurable, maximum width 2.7 mm.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 2.0 mm, interantennal isthmus 0.9 mm. Antennae reaching back beyond caudal margin of 2nd

tergite, relative lengths of antennomeres  $2 > 3 > 4 > 5 = 6 > 1 > 7$ . Genae without impressions. Facial setae as follows: epicranial, interantennal, subantennal, and genal absent, frontal 1-1, clypeal about 7-7, labral about 13-13. Process of mandibular stipes long, tip broadly rounded (Fig. 197).

Collum not extending below ends of following tergite. Paranota moderately depressed, continuing slope of dorsum, peritremata flattened; posterior corners rounded through segment 10, blunt on 11-14, becoming progressively more acute posteriorly.

5th sternum with low, rounded elevated areas between leg pairs, caudal ones larger and more widely separated; 6th sternum with knob-like processes between leg pairs, caudal ones longer and more widely separated. Postgonopodal sterna with distinct knob-like projections between 9th legs, narrowly segregated in midline; remaining sterna becoming progressively flatter and more plate-like posteriorly with progressively sparser hair patches adjacent to leg coxae. 2nd coxa with distinct, subconical anterior lobe and small caudal projection. Prefemoral lobes extending through segment 9.

Gonopodal aperture (Fig. 198, not this specimen) broadly ovoid, without caudolateral pouches, with moderate anterior indentation, 1.7 mm wide and 0.7 mm long at maxima; anterior indentation moderately long, subtriangular, apically rounded; sides not divided, gently curved, leaning slightly over opening, becoming slightly and progressively more elevated caudad, rims essentially smooth; caudolateral corner broad, slightly angled; caudal margin continuous with sides at caudolateral corner, elevation sloping rapidly to metazonal surface and terminating just beyond caudolateral corner, curving gently across midline; margins with only a few hairs arising from rims of elevations at caudolateral corners and adjacent parts of sides and caudal margin. Gonopods *in situ* (Fig. 198, not this specimen) with telopodites extending caudad in parallel arrangement along midline, extending just beyond caudal margin of aperture, tips directed dorsad. Gonopod structure as follows (Figs. 199-200): Telopodite short, terminating well before level of distal extremity of hairs. Prefemur short but proportionally long, about 7/8 of telopodite length, upright for most of length, trace of curvature distad, broad basally, tapering slightly distad, with three rows of continuous, regularly spaced hairs on inner surface and distomedial tuft of about 6 hairs. Acropodite short and broadly terminal, about 1/8 of telopodite length, continuous with, and poorly demarcated from, prefemur, continuing slight distal curvature of latter and directed dorsad, sides tapering rapidly to acuminate tip.

**Male paratype.** — Agreeing closely with holotype in all particulars.

**Female allotype.** — Fragmented, length unmeasurable, maximum width 2.4 mm. Agreeing essentially with males in somatic features, with following exceptions: Mandibular stipes with short, broadly rounded process. Sterna flat, with progressively sparser hair tufts adjacent to leg coxae on segments 4-7 and an occasional scattered hair thereafter.

Cyphopodal aperture elliptical, sides slightly elevated above metazonal surface. Cyphopods *in situ* (Fig. 201) with valves extending caudad along body axis, distal corners curved, protruding through opening. Valves (Figs. 202-203) moderate-size, subequal, distal corners extended, long, curved, and rounded, sides extending slightly around receptacle. Latter small, located on medial side of valves, submerged in and obscured by latter, invisible from caudal and anterior perspectives. Operculum small, tucked under free, dorsal side of valves.

**Variation.** — *Eurymerodesmus digitatus* undergoes considerable variation, and forms from Blanco



and Llano counties, adjacent to Burnet County, closely resemble the types. In these individuals, the aperture sides are higher, and in the Blanco County males, the elevation continues around the caudolateral corner for about 1/3 of the length of the caudal margin. The gonopods are very close to the types, but the corners of the cyphopod valves of Llano County females are not as elongate as those of the allotype.

The Travis County males display much wider apertures, and that from Elbow Cave (FSCA) is also much longer, extending nearly to the anterior segmental margin, thereby resembling the condition in *dactylocyphus*. The elevation is higher caudally on the sides, and in that from Elbow Cave, it begins abruptly at midlength on the sides, tapering nearly to the metazonal surface at the caudolateral corner. In one male from along Waller Creek, the sides lean noticeably over the opening, whereas in others from that site, the rim is flared laterad at the caudolateral corner. Except for the Elbow Cave male, the gonopods are very close to the holotype. In this individual the telopodites are longer, the prefemur curves more noticeably dorsad distally, and the acropodite does so even more strongly. Females are unknown from Travis County.

The Tarrant County males also display longer telopodites, extending to the level of the distal extremity of the hairs and farther from the aperture, terminating between the 8th legs. The mandibular process is shorter, broader, and subtriangular, and the cyphopod valves of females are not extended.

The Oklahoma males, found mixed in a sample with *mundus*, display a broader aperture with only slight elevation at the caudolateral corner. The mandibular projection resembles that in Tarrant County males.

*Ecology.* — Unknown. The vial labels lack indications of habitat, and nothing was mentioned in the original description.

*Distribution.* — A band along the boundary between the Central and Coastal Plains, extending from southwestern Oklahoma to central Texas near the Pedernales River (Figs. 176, 212). Specimens were examined as follows:

OKLAHOMA: *Comanche Co.*, Mt. Scott, 3M, 25 October 1974, G. Beck (MSU).

TEXAS: *Tarrant Co.*, Fort Worth, Normandy Dr., 20M, 24F, 4 juvs., 3 November 1979, G. Spicer (NCSM). *Burnet Co.*, 5 mi. ESE Marble Falls, 2M, F, juv., 15 February 1975, J. C. Loomis (FSCA, NMNH) TYPE LOCALITY. *Llano Co.*, 13 mi. SE Llano, 4M, 3F, 11 March 1961, J. F. Quinlan

(FSCA); and 27.8 mi. N Fredericksburg (Gillespie Co.), jct. TX hwy. 16 and 965, 10M, 13 March 1982, J. C. Cokendolpher (NCSM). *Blanco Co.*, 2 mi. N Johnson City, 2M, 13 March 1982, J. C. Cokendolpher (FSCA). *Travis Co.*, Austin, 4M, 5F, date and collector unknown (NMNH), and 4M, 19 November 1945, collector unknown (NMNH); along Waller Cr., 7M, juv., November 1963, J. Reddell (FSCA) and F, 9 April 1983, J. Reddell (TMM); and Elbow Cave, 3 mi. N Austin, M, February 1963, B. Russell (FSCA).

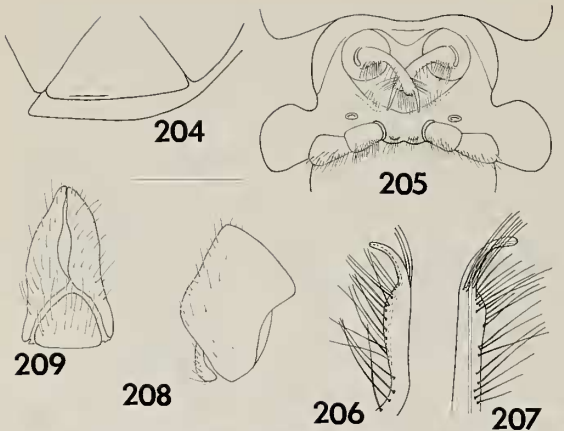
*Remarks.* — Chamberlin recognized that this form represented a new species and inserted a label stating "*E. austini* Chamb., Types" with the first sample from Austin, Travis County. However, this name was never validated and Loomis (1976) receives authorship credit.

*Eurymerodesmus digitatus* is similar to *melacis*, but differs in the genitalia of both sexes. The cyphopod valves are not elongate in *melacis*, whereas they are in the most proximate populations of *digitatus* with females. The gonopodal apertures are similar in general configuration, but that of *digitatus* is larger and the lateral elevation is more variable. The telopodites of *melacis* are uniform, and are longer and narrower than those of *digitatus*. The chief difference is the configuration and direction of the acropodite, which bends sharply laterad in *melacis* and curves gently dorsad in *digitatus*. This structure's curvature is slight in all males except that from Elbow Cave, Travis County, where it is stronger.

In contrast to *melacis*, there is little difference between *digitatus* and *sanbernardiensis*, and future collecting in Lee, Bastrop, Fayette, and Williamson counties may show them to be subspecifically related. For now I retain both names and distinguish them by the length and curvature of the acropodite, short and gently curved in *digitatus*, and longer and more strongly curved in *sanbernardiensis*.

Though differing in details of the gonopods, aperture, mandibular projection, and female cyphopods, I do not think that the differences between the populations of *digitatus* are of sufficient magnitude to warrant taxonomic recognition for forms in Travis and Tarrant counties, Texas, and Comanche County, Oklahoma. The last two sites are so widely separated from the type locality that differences could easily be bridged by forms from intervening areas.

As stated previously, the telopodites of *digitatus* are convergent with those of *dubius* as shown by comparing figures 47-48 and 199-200.



Figs. 204-209. *Eurymerodesmus clavatus*. 204, projection of left mandible of paratype, lateral view. 205, aperture and gonopods *in situ* of holotype, ventral view. 206, telopodite of left gonopod of the same, lateral view. 207, the same, medial view. 208, left cyphopod of female paratype, caudal view. 209, the same, medial view. Scale line for fig. 205 = 1.00 mm. Line for other figs. = 0.5 mm for each.

### *Eurymerodesmus clavatus*, new species

Figs. 176, 204-209, 212

*Type specimens*. — Male holotype and 7 male and 5 female paratypes (FSCA) collected by R. O. Albert, 3 February 1963, at New Ulm, Austin Co., TX. One male and one female paratypes deposited in NCSM.

*Diagnosis*. — A small species; males characterized by short mandibular projection; aperture moderate-size, much narrower than ventral segmental width; sides not divided, without caudolateral pouches, elevating slightly to caudolateral corners, descending to metazonal surface along caudal margin; telopodite short, barely overlapping caudal margin of aperture; acropodite moderately long, about 1/3 of telopodite length, narrowly terminal, arising solely from outer prefemoral margin; prefemur with many hairs arranged continuously along inner margin, expanding distad into clavate shoulder on inner margin; cyphopod valves of females with distal corners slightly extended; receptacle small, partly submerged in valves, sides not curving around operculum.

*Color in Life*. — Unknown.

*Holotype*. — Length 14.1 mm, maximum width 1.6 mm, W/L ratio 11.3%.

Somatic features similar to *hispidipes*, with following exceptions:

Width across genal apices 1.2 mm, interantennal isthmus 0.6 mm. Antennae reaching back to anterior half of 3rd tergite, relative lengths of antennomeres 2>3>6>5>4>1>7. Genae without impressions. Facial setae as follows: epicranial 1-1, inter-

antennal, subantennal, and genal absent, frontal 4-4, clypeal about 9-9, labral about 14-14. Process of mandibular stipes short, subtriangular, apically acute (Fig. 204).

Collum not extending below ends of following tergite. Paranota moderately depressed basally, continuing slope of dorsum, peritremata somewhat flattened; posterior corners blunt on segments 1-3, rounded on 4-7, blunt on 8-13, becoming progressively more acute posteriorly.

5th and 6th sterna with small hirsute areas adjacent to leg coxae but without lobes or projections. Postgonopodal sterna with flattened hirsute areas adjacent to 9th coxae; remaining sterna becoming flatter, more plate-like, and less hirsute caudally. 2nd coxa without lobes, gonapophyses relatively long, extending to near midlength of 4th sternum. Prefemoral lobes small, not pronounced, extending through segment 8.

Gonopodal aperture (Fig. 205) small, heart-shaped, without caudolateral pouches, with moderate anterior indentation, 0.7 mm wide and 0.3 mm long at maxima; anterior indentation moderate-size, broadly triangular, apically rounded; sides not divided, angling strongly mediad, becoming slightly elevated caudad, rims smooth; caudolateral corner poorly defined, indistinct, continuous with lateral curvature; caudal margin continuous with sides, angling to point in midline, slightly elevated and thickened at approximate location of caudolateral corner, flush with segmental surface in midline; margins nearly glabrous, with only 6 or so hairs on thickening at caudolateral corner. Gonopods *in situ* (Fig. 205) with telopodites crossing in midline and extending slightly over opposite side of aperture. Gonopod structure as follows (Figs. 206-207): Telopodite terminating just before level of distal extremities of hairs. Prefemur proportionally short, about 2/3 of telopodite length, upright but with slight bisinuate curve, relatively narrow basally, expanding near midlength and continuing distad into broad shoulder on inner margin, with two rows of continuous, regularly spaced hairs on inner surface and distomedial tuft of about 6 hairs. Acropodite proportionally long and narrowly terminal, about 1/3 of telopodite length, arising from outer prefemoral margin, discontinuous with and sharply demarcated from prefemur, curving broadly dorsad, sides tapering smoothly and continuously, expanding slightly apically, tip rounded.

*Male paratypes*. — The only variation of the male paratypes is that the telopodites *in situ* sometimes extend well beyond the caudal aperture margin, terminating over the sternum between the 9th legs. The structure and configuration of the aperture and gonopods are as described for the holotype.

*Female paratype*. — Length 15.8 mm, maximum width 2.6 mm, W/L ratio 16.5%. Agreeing essentially with holotype in somatic features, with following exceptions: Subantennal setae 1-1, frontal 2-2, genal 2-2, clypeal and labral series merging and continuing for short distances along genal borders, about 4 setae per side. Mandibular stipes without projection, corner not produced. Sterna flat, glabrous. Prefemora without lobes.

Cyphopodal aperture relatively broad, ovoid, sides elevated above metazonal surface, caudal margin elevated laterally, more so in midline, flared caudad. Cyphopods *in situ* with valves oriented transversely in aperture, tips visible. Valves (Figs. 208-209) moderately large, subequal, corners slightly extended, with lobe on ventral surface. Receptacle small, located laterad to valves at bases, partly submerged in latter. Operculum proportionally large, clearly visible on medial side of valves.

*Ecology*. — Unknown.

*Distribution*. — Known only from the type locality (Figs. 176, 212).



*Remarks.* — The narrowly terminal, discontinuous acropodite, sharply demarcated from the prefemur, resembles the condition in *simplex*, except that it arises from the outer prefemoral margin rather than the inner. Accordingly, the distal prefemoral shoulder is on the inner surface instead of the outer. Thus, there is no question that the narrowly terminal condition in *clavatus* is convergent with that in *simplex*.

#### ECOLOGY

With so little field experience with eurymerodesmids, I cannot generalize about habitat preferences and can only report in the individual accounts my observations of the few species I have collected. However, information on vial labels and in the literature suggest that eurymerodesmids may seek shelter under almost any object in a wide array of biotopes ranging from sandy, predominantly pine Atlantic coastal habitats, to deciduous forests in the southeast and the Ouachita, Ozark, and Central Lowland Provinces, to grasslands of the Great Plains, and to xeric desertine environments of the Edwards Plateau. They often seek shelter in caves.

I was struck by the difficulty I had in finding them and by how spotty their occurrences can be. With all the winter trips that I have made to Florida, I have only encountered *v. varius* four times, and the only place that I have found it farther north is the North Carolina site. The available records suggest that it is common in the southeast, yet I have collected extensively in Alabama, Georgia, and the Carolinas at the proper time of year without even one accidental discovery. Conversely, local populations can be very large; for example, populations of *v. varius* can be in the hundreds if not thousands of individuals. The populations I discovered in Alachua and Duval counties, Florida, and Robeson County, North Carolina, were easily this large, and I could have taken far more specimens. Sizeable pitfall samples were also obtained from Leon and Jefferson counties, Florida, and there is a very large sample of *v. christianus* from Washington Parish, Louisiana. These aggregates suggest that *varius* would be a suitable subject for population studies.

Likewise in south Texas, *melacis* can be locally abundant. I could have taken many more individuals at the Welder Wildlife Refuge, San Patricio County, and two samples from Hidalgo and Kerr counties are quite large. The patchy distribution was evident at the Refuge, where I found *melacis* in several small thickets around the office buildings but not in

similar thickets on the range. Nor did I encounter additional specimens anywhere in south Texas despite searching out similar environments and working in general areas where I knew it occurs. North of Texas and Louisiana I have only collected one eurymerodesmid, *oliphantus* from Jackson County, Illinois, despite considerable work in forests in the Ozarks and Mississippi Valley, where they are abundant judging from the extensive collections at the FSCA. In summary, I have had little success in finding eurymerodesmids anywhere, so if there is a secret to collecting them, as there is with American platyrhacids and cove-dwelling Appalachian species of *Sigmoria* (Shelley 1981, 1982; Shelley and Whitehead 1986), I have not deduced it.

According to Wood (1867), the type specimens of *impurus* were discovered under old cow dung, and Causey (1952a) remarked that two or three milliped species may be found under a single piece of dung since there is little other cover. This statement seems plausible, but I did not find a single eurymerodesmid under dung during two weeks in Texas in February 1986. I turned scores of piles in all stages of decay and dessication, but *Desmonus* (Sphaeriodesmidae) was the only polydesmoid that I encountered. The



Fig. 210. Seasonality of *Eurymerodesmus*; the number of samples with adults per month.

few eurymerodesmids that I discovered in Texas were all under fallen logs and branches.

Throughout their distribution, eurymerodesmids demonstrate marked seasonality, showing a distinct preference for the cooler months of spring, autumn, and winter. Thus, they probably will not be encountered in the summer, which explains why I only found exoskeletal fragments of one male in Texas and the Ozarks in July 1980. To illustrate this phenomenon, I combined the species and plotted the samples from each month with at least one adult (Fig. 210). Although this probably reflects field activity to some degree, I think it portrays their availability reasonably accurately. Many other millipeds have been collected in the eurymerodesmid range in the summer, so many more samples would be expected from May-September if the millipeds were present. December was the most productive month for eurymerodesmids, followed by April, February and March, November, and October. Eleven fewer samples were taken in January than in October, but 24 more than in May. Thus, the seven coolest months of the year provided 90.9% of the preserved eurymerodesmid samples with adults. Future field investigations should therefore be concentrated in these months.

#### DISTRIBUTION

*Family and genus.* — Except for the Ozark and Ouachita Provinces in Arkansas and Missouri, the Eurymerodesmidae is a lowland milliped family occurring in the Coastal Plain, Central Lowlands, and Great Plains Physiographic Provinces (Fig. 1), the regions of the central, south-central, and southeastern United States with the least topographical variation. The center of diversity lies in the Coastal Plain of southern Arkansas and northern Louisiana, extending northward into the southern fringe of the Ouachita Province. Fourteen of the 25 species, 56.0% of the total known fauna, are represented there as are three of the four lineages and six of the seven species groups, the *melacis* lineage and group of Texas and southwestern Oklahoma being the sole exceptions (Figs. 211, 213, 214). The range spans such major rivers as the Pee Dee, Santee, Savannah, Chattahoochee, Alabama, Pearl, Mississippi, Sabine, Brazos, Colorado, San Antonio, and Nueces. Inland it traverses the Red and Arkansas/Canadian Rivers, two major tributaries of the Mississippi, and the southwesternmost record, the Terrell County, Texas, locality of *melacis*, is just west of the Pecos River near its confluence with the

Rio Grande. In figure 1 a smooth curve is drawn around range extremes in all directions, except for the area north of the Missouri River in northern Missouri and southern Iowa. No authentic records are known from north of this watercourse, which appears to be a boundary in this part of the range. Consequently, *Eurymerodesmus* probably does not protrude into southeastern South Dakota. The irregular northern boundary indicates three separate penetrations that extend progressively farther north: one along the Atlantic Coastal Plain into southeastern North Carolina and two in the Central Lowlands Province into central Illinois and north-

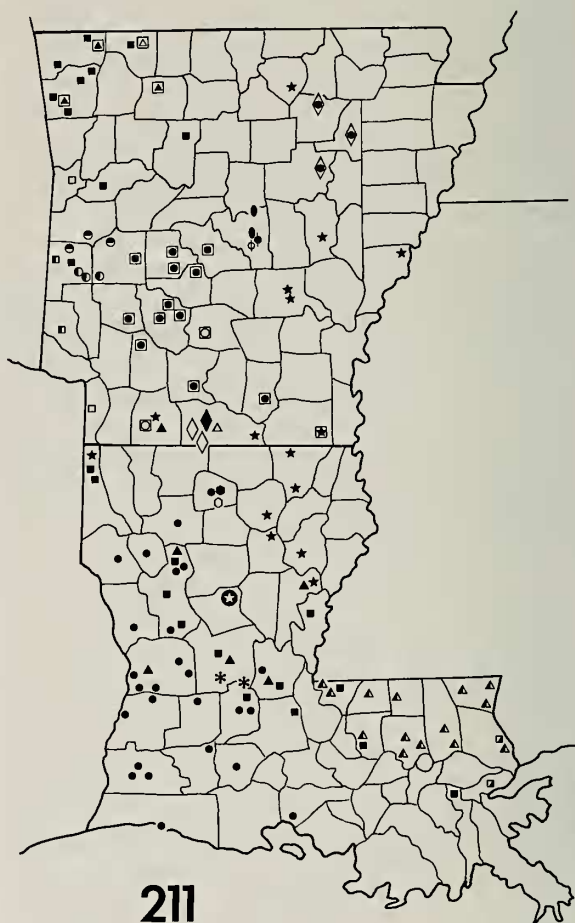


Fig. 211. Distributions of species of *Eurymerodesmus* in Arkansas and Louisiana. Star in square, *hispidipes*; stars, *angularis*; diamonds, *compressus*; vertical half-shaded dots, *goodi*; dots/circle in square, *dubius*; half-shaded triangles, *varius christianus*; triangles, *varius louisianae*; dots, *amplus*; triangles in squares, *neytonus*; dots in diamond, *oliphantus*; asterisks, *simplex*; horizontal half-shaded dots, *polkensis*; hexagons, *parovicus*; star in dot, *crassatus*; dot/circle with line, *pulaski*; ovals, *serratus*; squares, *birdi birdi*; diagonal half-shaded squares, *birdi planus*; vertical half-shaded squares, *mundus*. Open symbols denote literature records considered reliable.



eastern Nebraska. The southern boundaries are the Rio Grande, since no authentic records are known from adjoining parts of Mexico, the Gulf of Mexico, and the southern limit of the mesic deciduous woodlands in Florida, as discussed in the *v. varius* account. However, little sampling has taken place in potential sections of Coahuila, Nuevo Leon, and Tamaulipas states, so there is a reasonable probability of future Mexican discoveries.

Boundaries in other areas are less precise, but from my own field investigations, I doubt if *Eurymerodesmus* extends much farther west in Texas, or north in North Carolina. As discussed in the *melacis* account, I unsuccessfully turned countless logs and sifted through considerable litter and debris around Lubbock, Texas, and in the Davis

Mountains in February 1986, so if *eurymerodesmids* occur in the panhandle or southwestern Texas, it is difficult to imagine where they could be other than in caves or remote, secluded ravines. Southeastern North Carolina, the area of the northernmost record along the Atlantic Coast, has been sampled extensively in all seasons of the year by biologists at the NCSM with only the one discovery of *v. varius*. I have personally searched for this species many times in the southeastern quadrant of the state, and exhaustive field work has been conducted by NCSM personnel throughout the Coastal Plain and well into southeastern Virginia. Consequently, the presently known limit, about eight miles north of the South Carolina border, is probably very close to the actual one.

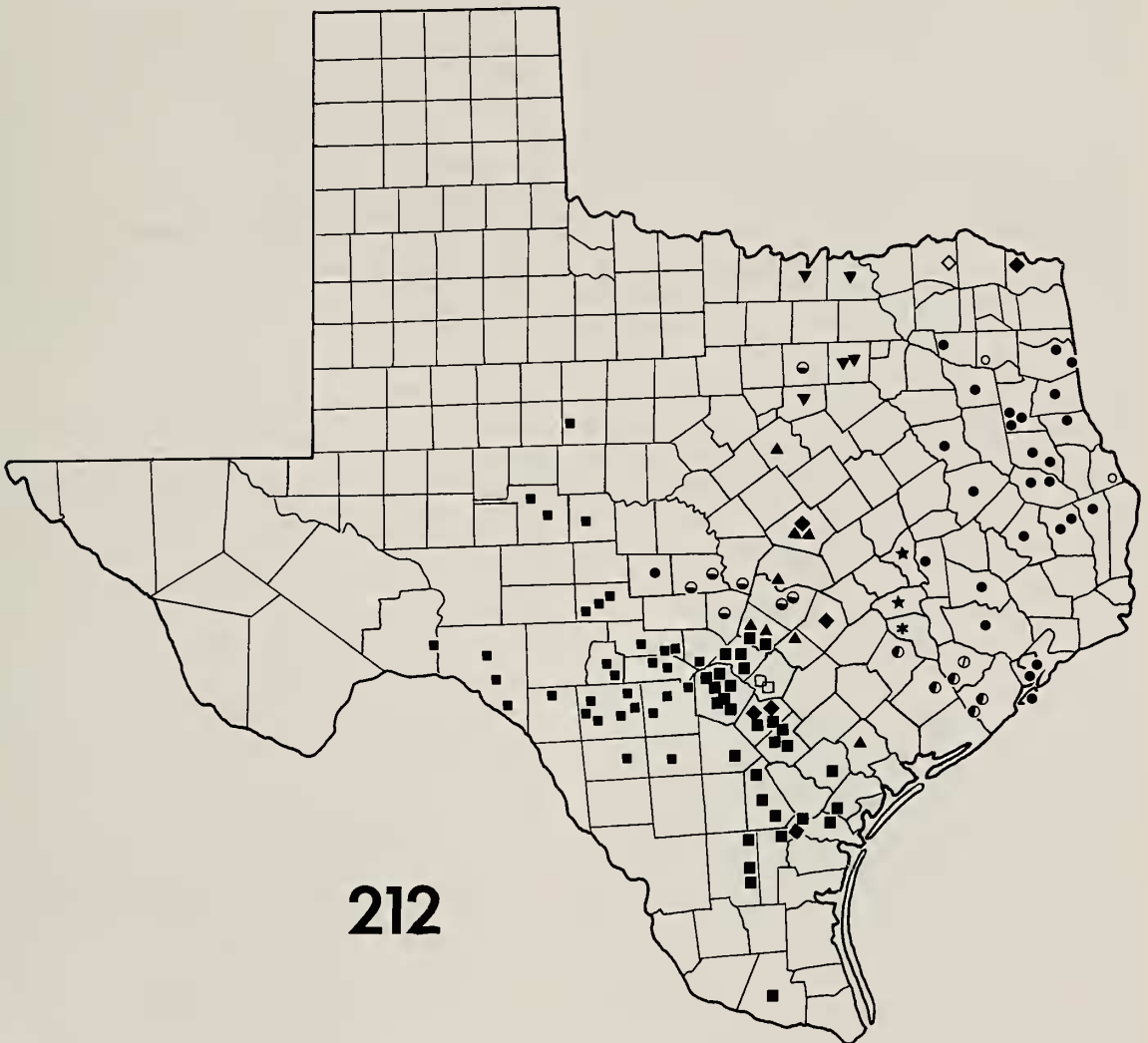


Fig. 212. Distributions of species of *Eurymerodesmus* in Texas. Stars, *impurus*; dots, *amplus*; diamonds, *birdi birdi*; inverted triangles, *mundus*; squares, *melacis*; upright triangles, *dactylocyphus*; verticle half-shaded dots, *sanbernardiensis*; horizontal half-shaded dots, *digitatus*; asterisk, *clavatus*. Open symbols denote literature records considered reliable.

Other peripheries have not been thoroughly investigated, but the western boundary in the plains states and the inland periphery in the southeast are considered reasonably accurate. The limit in Kansas approximates that of the xystodesmid *Pleuroloma flavipes* Rafinesque (Shelley 1980), which in turn correlates roughly with the western terminus of the Central Lowland Physiographic Province. The interior boundary in the southeast is generally the Fall Zone region between the Coastal Plain and Piedmont Plateau Physiographic Provinces. Such inland records as Macon, Georgia, and Auburn, Alabama, are in the Fall Zone, and there are no definite localities from the Piedmont Plateau in any state. The only regions where the boundaries are nebulous are northern Illinois, and Kentucky and Tennessee. Field work in Illinois has focused on the Shawnee National Forest in the south, but the record of *hispidipes* from Coles County, in east-central Illinois, suggests occurrence into northern Illinois, perhaps even to metropolitan Chicago if the range extends to the same latitude as *mundus* in Nebraska. Eastward expansion into western Indiana is not implausible, although the Wabash River may restrict it from the southwestern corner of this state. Thus, collecting in central Illinois and adjacent Indiana could significantly expand the family's range. No specimens have been taken from western Kentucky and Tennessee, so the line in these states is hypothetical, connecting records from Illinois and Mississippi; the family is not known to traverse the lower Ohio River as figure 1 shows. However, eurymerodesmids may be logically anticipated in the shaded areas of Kentucky and Tennessee, and perhaps as far east as the western loop of the Tennessee River.

*Species, species groups, and lineages.* — The *hispidipes* lineage, comprised of the single species and group, is known definitely from only two sites some 470 miles apart, one in east-central Illinois and the other in southern Arkansas (Figs. 9, 213, 214). This distance is so great as to virtually preclude extant connection. The *impurus* group (Figs. 9, 213) covers most of Arkansas except the northwest corner. It swings broadly through northern Louisiana with outlying records from eastern Mississippi, west-central Missouri, and east-central Texas. The Missouri and Mississippi forms are judged conspecific with those in Arkansas, and I connect these areas by a single line in figure 213. However, the species in Texas, *impurus* itself, has a different aperture with false pouches, and is shown as isolated (Fig. 213). The intervening area in eastern and north-

eastern Texas should be sampled in detail to determine if the areas connect geographically and whether anatomical connection can be demonstrated between the true pouch of *angularis* and that of *impurus*.

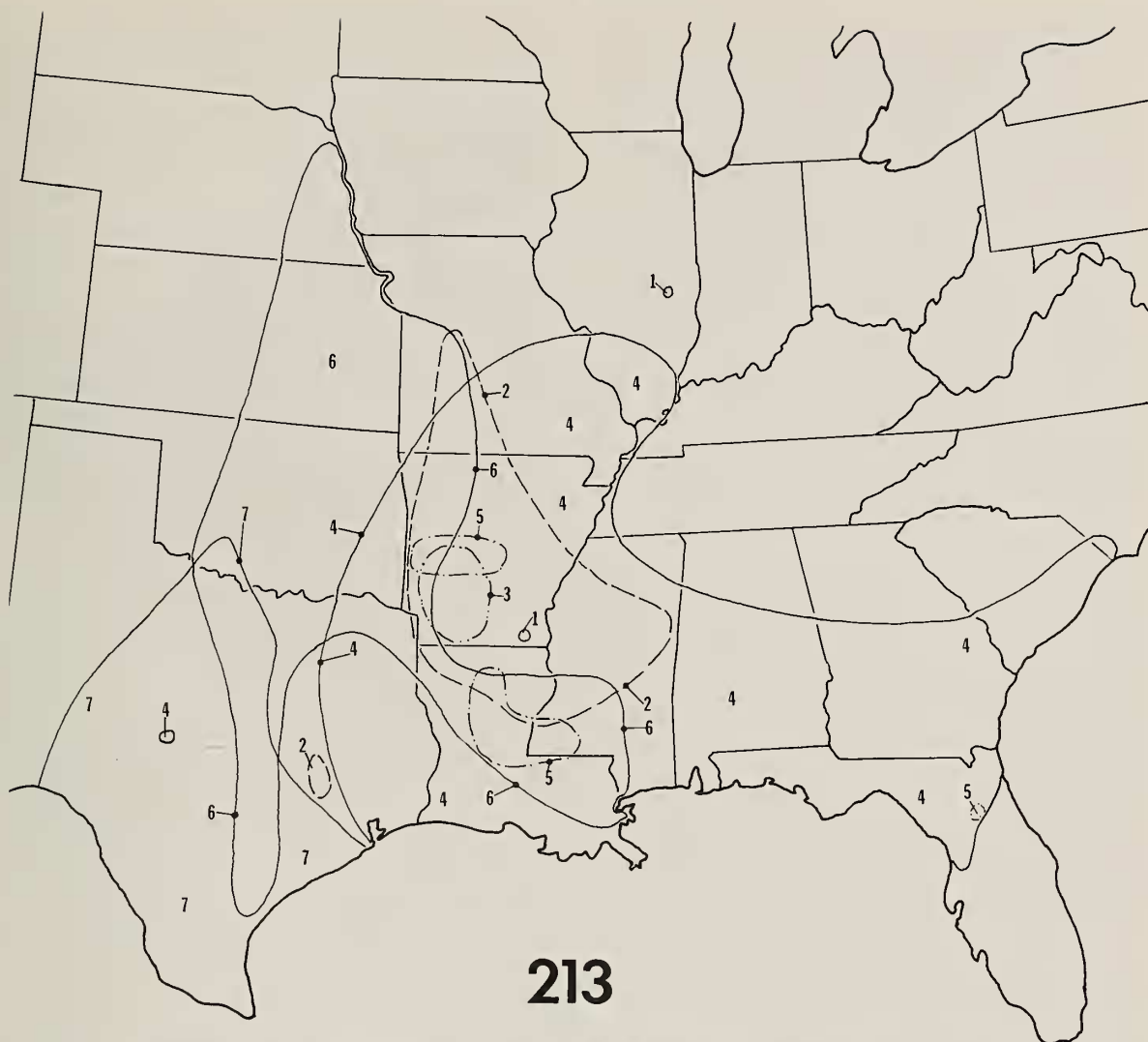
The *varius* group is the easternmost and most widely ranging species group, although much of the area is occupied by a single species, *varius* (Figs. 54, 213). South of the Ohio River, *varius* is the only component east of the Mississippi, and it also extends into western Louisiana and southern Arkansas. The northern part of the group's range, in Illinois, Missouri, and Arkansas, contains sizeable lacunae that need to be explored, although I show it as continuous in figure 213. Gonopodal similarities between *amplus*, *newtonus*, and *elevatus* suggest a continuous fauna from southern Louisiana and eastern Texas through central Missouri, and the close resemblance between all males of *oliphantus* suggests continuity between its four known areas. However, I show the westernmost record of *amplus*, from Mason County, Texas, as a small, separate area in central Texas (Fig. 213) because of the size of the intervening gap, about 190 miles, and the absence of similar forms to the north and south. The *varius* group should be expected in eastern Oklahoma, where it is currently unknown; the proximity of *newtonus* to northeastern Oklahoma suggests occurrence in Delaware, Adair, and possibly Cherokee counties.

The *simplex* group contains seven localized clusters of records, six of which comprise a reasonably compact unit in southern Arkansas, northern Louisiana, and southwestern Mississippi, although much more sampling is needed (Figs. 54, 213). The seventh area, representing an allopatric population of *serratus*, is far to the southeast in Alachua County, Florida. This site and the type locality of *caesariatus* are the only records of the *simplex* group from east of the Mississippi River, and they suggest a substantial fauna with numerous undiagnosed forms along the Gulf Coast in the Florida panhandle and southern Mississippi and Alabama.

The *dubius* group, the fourth and only monobasic group in the *Kewanius* lineage, inhabits a broad, contiguous area in southern Arkansas, where it is known from many counties (Figs. 211, 213). It may occur in northwestern Louisiana and, conceivably, even the northeast corner of Texas.

Because it is the most diverse assemblage in *Eurymerodesmus*, combining the *impurus*, *dubius*, *varius*, and *simplex* groups, the *Kewanius* lineage expectedly occupies the greatest area, around 2/3 of





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Fig. 213. Comparative distributions of the species groups of *Eurymerodesmus*. 1, *hispidipes* group; 2, *impurus* group; 3, *dubius* group; 4, *varius* group; 5, *simplex* group; 6, *birdi* group; 7, *melacis* group.

the generic range (Fig. 214). It is the easternmost lineage, covering all the area in the southeast, and it expands northward along the Mississippi Valley into Illinois and Missouri, and westward through Arkansas and Louisiana into eastern Texas and, by implication, eastern Oklahoma. It overlaps the eastern half of the *birdi* lineage and the Arkansas site of *hispidipes*, and its allopatric population in central Texas is sympatric with the *melacis* lineage. No overlap is otherwise known between the *Kewanius* and *melacis* lineages, which appear to be parapatric in southeastern Texas.

The *birdi* lineage is the northernmost ensemble, occupying the western periphery in the northern sector of the range (Figs. 147, 213, 214). It extends in a wide band from Nebraska and western Missouri into

northeastern Texas, where it divides into a broad branch that penetrates across the Mississippi River into southeastern Louisiana and southwestern Mississippi, and a narrow branch that continues into south Texas. This is the most continuous assemblage in *Eurymerodesmus*, but populations of *b. birdi* in south Texas are some 214 miles from the closest records in northeastern Texas. The gap is filled by *mundus*, lending continuity to the lineage's distribution. Aside from this hiatus in *b. birdi*, there are no areas where collecting is particularly needed in the *birdi* lineage, although pinpointing the western and northern extremities would be useful.

The *melacis* lineage, the southernmost and westernmost assemblage, occupies the southwestern periphery of the genus (Figs. 176, 213, 214), over-

lapping the southern extension of the *birdi* lineage and the westernmost site of *Kewanius*. It extends from the Gulf of Mexico onto the Edwards Plateau in south-central Texas, with the inland or western border pushing northward into Oklahoma, while the coastal boundary lies south of Houston and is parapatric to the *Kewanius* lineage. Records are concentrated east of highway I-35, north of I-37, and between San Antonio and Del Rio. Little material is available from south Texas, and there is a large gap in the north-central area, where the Fort Worth record of *digitatus* is the only one between Comanche county, Oklahoma and the type locality in Burnet County, near the latitude of Austin. Because of the Fort Worth record I show a unified area for the *melacis* lineage in (Figs. 213-214), but the record

in the Wichita Mountains of Oklahoma may be detached from the rest of the range. Considerable field work is therefore needed in the area bounded by the Wichita Mountains on the north, I-35 on the east, Burnet and Llano counties, Texas, in the south, and Abilene on the west.

Although the range of the Eurymerodesmidae is far from thoroughly collected and many distributional gaps remain, some lacunae between con-specific populations are so large as to virtually guarantee allopatry. For example, gaps of over 150 miles occur in *hispidipes*, *angularis*, *varius*, *amplus*, *serratus*, *birdi*, and *digitatus*. The largest hiatus is in *serratus*, where the Pulaski County, Arkansas, and Alachua County, Florida, populations are segregated by over 700 miles. Because of the vastness

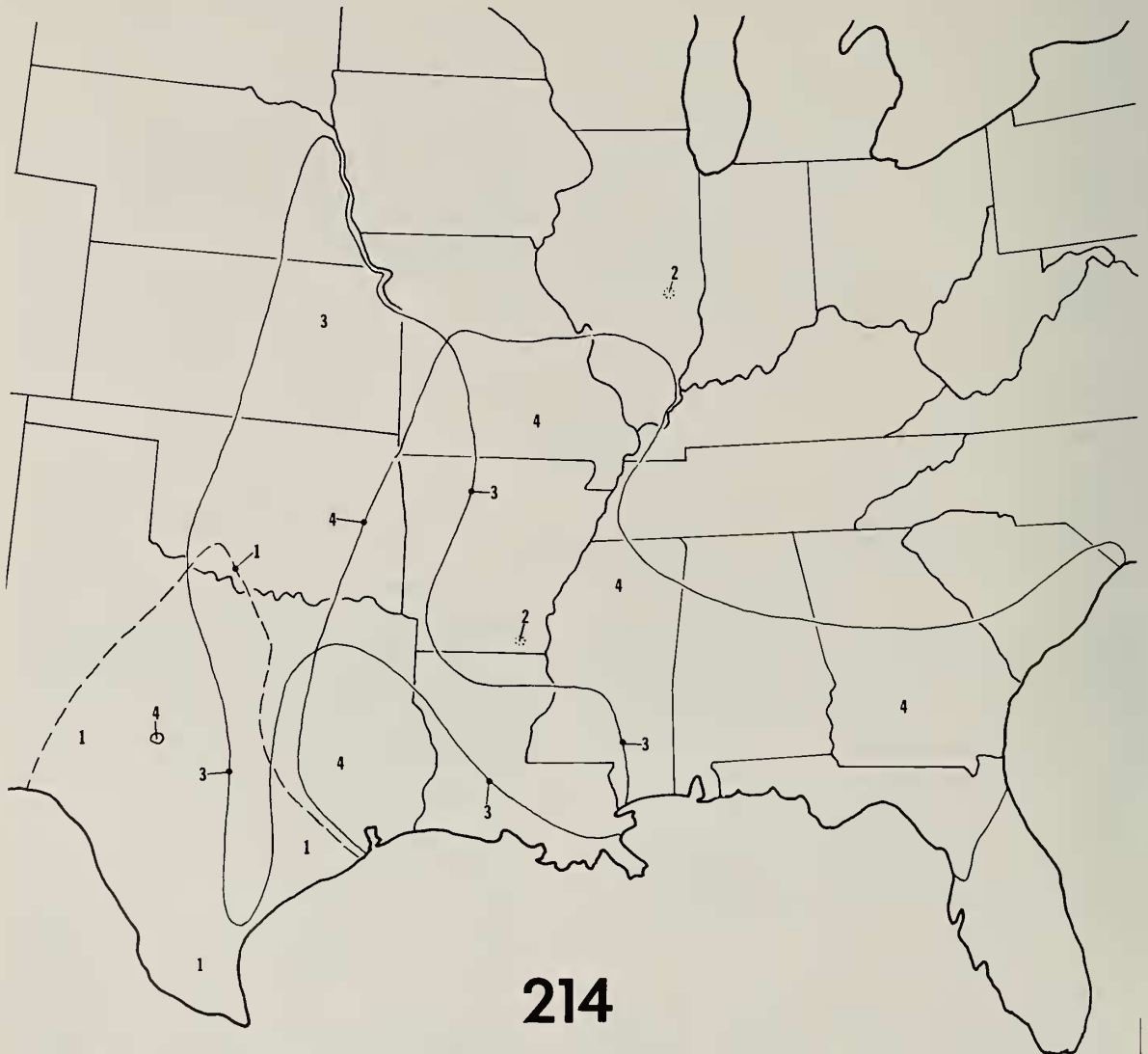


Fig. 214. Comparative distributions of the lineages of *Eurymerodesmus*. 1, *melacis*; 2, *hispidipes*; 3, *birdi*; 4, *Kewanius*.



of the intervening region, which covers more than three states, it is hard to imagine that these populations connect today. Likewise in *hispidipes*, there is a hiatus of around 470 miles between the known populations, a sizeable gap suggesting absence of extant connection. The allopatric population of *amplus* in grasslands of the Edward's Plateau in Mason County, Texas, is isolated from the bulk of the range in forested eastern Texas by some 190 miles. In contrast to the preceding species, there are five allopatric records of *b. birdi* from four non-contiguous counties in south-central and southern Texas, the northernmost of which is about 215 miles south-southwest of the main area of the race in Oklahoma, northeast Texas, and Louisiana. These four counties are at least 70 miles apart and their localities may or may not interconnect, but together they appear detached from the rest of the range. Consequently, *b. birdi* seems to consist of two populations — a relatively continuous one extending from eastern Missouri and eastern Kansas through Oklahoma, western Arkansas, and northeastern Texas to the vicinity of New Orleans, and a smaller, subcontinuous one in southern and south-central Texas, ranging at least from Bell to San Patricio counties. The dimensions of the latter cannot be approximated from present knowledge, but it could be relatively large, encompassing much of the area from Corpus Christi and Victoria on the coast to San Antonio, Austin, and Belton inland.

The widely allopatric records of *angularis*, *v. varius*, and *digitatus* are more likely to be joined by future collecting, either because the lacunae are smaller, or the habitat is more uniform, or both. My reasoning is largely intuitive, but I have considerable field experience in the 275 mile gap in *v. varius* between Macon, Georgia, and Robeson County, North Carolina. I do not think that there are nearly enough differences between coastal environments in Georgia and the Carolinas for the latter populations to be isolated. This hiatus is logically a collecting artifact that will eventually be filled with material from South Carolina.

*Future work.* — I conclude this discussion of distribution with a review of future collecting needs. Beginning in the southeast, efforts are needed to connect the Florida and Arkansas populations of *serratus*, but it is impossible to predict where additional discoveries may be made. They are more likely in Mississippi since the eurymerodesmid fauna there is more diverse than in states to the east, where *v. varius* is the only known form aside from the one *serratus* record. Otherwise, the only future field

work that is really needed east of Mississippi is material of *v. varius* from the void in South Carolina and preferably also eastern Georgia.

Meticulous field sampling, perhaps to the extent of spending two to three days in each county, is needed from central Mississippi through Louisiana and Arkansas, the region of greatest species diversity. Many more forms undoubtedly occur there, particularly in the *simplex* group. The record of *angularis* from Oktibbeha County, Mississippi, needs to be linked with the rest of the range in Arkansas and Louisiana, which should be thoroughly collected to determine the relative statuses of the various forms with long acropodites. Emphasis should be placed on Union and Columbia counties, Arkansas, to determine boundaries of *compressus*, and topotypes of *Paresmus columbus* are needed from Magnolia, in the latter county, to confirm or disprove its synonymy with *dubius*. Careful sampling is also needed in Pulaski County and environs to ascertain distributions of *pulaski* and *serratus*, which were mixed in Bollman's material (NMNH), and forms between Montgomery and Pulaski counties may tie *serratus* and *polkensis* together. Collection needs dwindle to the south and north, except for more material of *simplex* around Evangeline Parish, Louisiana, and *newtonus* in northwestern Arkansas. Specimens from central Missouri will delineate the range of *elevatus* and possibly connect it with *newtonus*, as well as close the hiatus of 216 miles in *angularis*.

In the northern part of the range east of the Mississippi River, efforts are sorely needed in central Illinois to secure more material of *hispidipes*, determine its distribution, and pinpoint the northern periphery of the family in this area. South of the Ohio River, *Eurymerodesmus* should be documented from western Kentucky and Tennessee, where new forms may be encountered.

The northern and western peripheries of the family in Nebraska and Kansas need refinement, but the only specific collecting needs are corroboration of early literature records of *b. birdi* and *mundus* as explained in their accounts. A few literature records of these species also need confirmation in Oklahoma, but the principle requirement is in the eastern, Ouachita section. *Eurymerodesmus newtonus*, *goodi*, and *polkensis* all occur just across the state line in Arkansas and can be anticipated in eastern Oklahoma, where only *b. birdi* and *mundus* are currently known. In southwestern Oklahoma, more material is needed of *digitatus* in and near the Wichita Mountains and southward to the Red River.

Considerable field work is needed in Texas, with emphasis on the void between Abilene and Fort Worth, and Wichita Falls and Llano/Burnet. No specimens, not even juveniles, have been taken from this substantial area where eurymerodesmids can be expected to be abundant and *digitatus*, *melacis*, and *mundus* may occur. East Texas has been comparatively well collected, based on the number of samples of *amplus*, but more work is needed to try to link *impurus* in Brazos County with the rest of its group in northwestern Louisiana. Marion and Harrison counties should harbor *angularis*, based on its occurrence in Caddo Parish, Louisiana, and additional representatives of the *impurus* group may exist around Nacogdoches, Huntsville, and the Big Thicket Area, where only *amplus* is currently known. South of Houston, male topotypes are still desired for *sanbernardiensis*, to eliminate doubt of its identity. In addition to more individuals of *impurus*, detailed collecting in neighboring Colorado, Waller, Austin, Washington, and Fayette counties may provide more individuals of *clavatus* and clarify the relationship between its unique gonopod and the rest of the *melacis* group. Farther south, material is needed from the slight gaps in the range of *dactylocyphus* in Gonzales and Dewitt counties, in addition to those farther north in Travis and Corzell counties. The range of *melacis* in south Texas is the best collected area of the state, but additional specimens are needed along the southern Rio Grande in the vicinities of Eagle Pass, Laredo, Hebbronville, Zapata, and Rio Grande City.

For the benefit of future workers and to complement the group and lineage range maps, I append county distribution maps for the states with the most diverse faunas, Arkansas, Louisiana, and Texas (Figs. 211-212). Except for north-central and north-eastern Arkansas and the southernmost part of Louisiana, the first two states are reasonably covered with records, but larger voids exist in Texas, which, because of its greater area, could alone take several years to adequately sample. Add another two or so years for systematic field investigations in Arkansas and Louisiana, and perhaps five or more years can be spent in just these three states. When the additional time for studies in other areas is considered, it becomes obvious that research on the Eurymerodesmidae has just begun. Many questions remain to be answered, and the present system of species groups and lineages may need to be completely revamped when significantly more material is available.

## RELATIONSHIPS

*Family and genus.* — The great enigma surrounding the Eurymerodesmidae is its phylogenetic affinities. There are suggestions that it is a recent derivative of the Xystodesmidae (Hoffman 1978, 1979), an appealing idea because of the close similarity in body form. Possible synapomorphies with the Xystodesmidae include the short, cylindrical, truncate gonapophyses and the gently curved to bisinuate tarsal claws, which appear to be slightly specialized because of the basal swellings. There are also similarities with the Holistophallidae, some forms of which have elaborate gonopodal apertures and strong anterior indentations. However, this family is poorly known, and the aperture traits are not manifested by all components. The constricted aperture is also associated with its modified gonopods, and thus is not homologous to that in the Eurymerodesmidae. Until family relationships are resolved, I regard the Xystodesmidae and Eurymerodesmidae as sister taxa within the Xystodesmoidea.

Apparently on an empirical basis, Hoffman (1979) arranged the Chelodesmoidea as follows:

Superfamily Chelodesmoidea: Family  
Chelodesmidae.

Superfamily Xystodesmoidea: Families  
Xystodesmidae, Eurymerodesmidae,  
Gomphodesmidae, Campodesmidae,  
and Oxydesmidae.

Superfamily Sphaeriodesmoidea: Families  
Sphaeriodesmidae, Holistophallidae.

Superfamily Platyrrhacoidea: Family  
Platyrrhacidae.

Superfamily Rhachodesmoidea: Families  
Rhachodesmidae, Tridontomidae.

The Campodesmidae, Holistophallidae, and Tridontomidae were said to have around 8, 11, and 3 known species, respectively, while the Eurymerodesmidae, with 25 known species, is the smallest of the more speciose families. Most of these taxa have now been subjected to reasonably intensive studies, and the least investigated, the Sphaeriodesmidae, Holistophallidae, and Rhachodesmidae, may hold keys to subordinal affinities as may the western Nearctic xystodesmids in the tribes Harpaphini and Chonaphini, which lack the characteristic prefemoral spines found in Central American and eastern Nearctic tribes.

*Species, species groups, and lineages.* — Discussion of relationships within *Eurymerodesmus* is tentative because of the large number of unknown



forms that obviously await discovery. Since it will probably be decades before substantially more material is available, it is appropriate to draw conclusions from the present data. Accordingly, I present (Fig. 215) a preliminary diagram of relationships among the lineages. Unique features can be suggested only for the *melacis* branch — short telopodites, either wholly enclosed within the aperture or only slightly overlapping the caudal margin, and relatively nondescript apertures with margins usually flat or only slightly elevated — and I judge them to be plesiomorphies, although determination of polarity is hampered by incomplete knowledge of potential outgroups. Nondescript apertures are also contradicted by *dactylocyphus*, which has a broad, distinctive opening with substantial flange-like elevations at the caudolateral corners in some forms. However, neither of these traits appears in other lineages, in contrast to the characteristic lobes of the *birdi* branch, also displayed by *polkensis*, and to lesser extents *pulaski* and *serratus*, all of the *Kewanius* line. The lobes of the *birdi* lineage also are not shared by all of its components. They are absent from *birdi planus*, whose type population has a nondescript aperture like those in the *melacis* branch, a similarity reflecting convergence. Despite these difficulties, I think that *Eurymerodesmus* can be divided into these four lineages or major components, three of which, like the subgenera of *Sigmoria* (Shelley and Whitehead 1986), display geographic cohesiveness. They are undeniable geographic entities and defensible from the standpoint of geography. The exception is the *hispidipes* branch, comprised of a unique species from two allopatric populations, which does not fit in another line.

I placed *polkensis*, *pulaski*, *serratus*, and *caesariatus* in the *simplex* group, *Kewanius* lineage, because all have narrowly terminal or subterminal acropodites. However, they could equally well go in the *birdi* lineage if greater weight were placed on the aperture. The first three species possess undivided apertures with variable elevations on the caudal margins (Figs. 109, 114, 134, 137, 142, 146), whereas *simplex*, *paroicus*, and *crassatus* exhibit divided apertures with caudolateral pouches (Figs. 103, 123, 127). In particular, *polkensis* has strong subtriangular lobes (Figs. 109-110), very much like those in the sympatric form of *b. birdi* (Figs. 157-158). Likewise in Mississippi, the largely unadorned aperture of *caesariatus*, with only very slight, indistinct elevations at the caudolateral corners (Fig. 117), is shared with proximate forms of *birdi planus* (Figs.

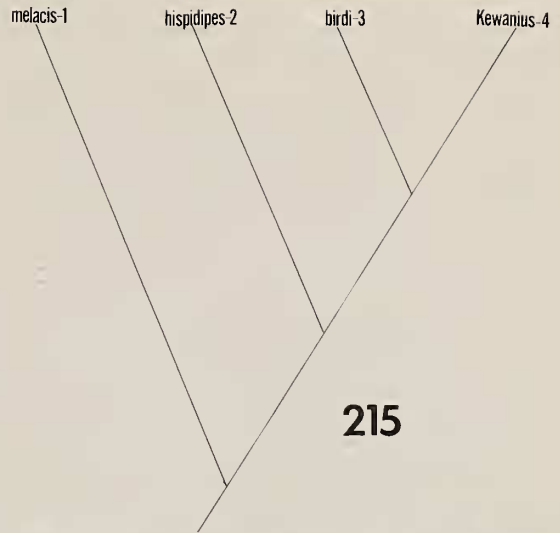


Fig. 215. Relationships of lineages in *Eurymerodesmus*. The numbers refer to figure 214.

162, 165). Thus, these four species combine features of the *simplex* and *birdi* groups in the gonopods and aperture, respectively, and the undivided apertures of *goodi* and *dubius*, of the *impurus* and *dubius* groups, may also reflect genetic influence of *birdi*. Thus as with the subgenera of *Sigmoria*, the *birdi* lineage is a distinct geographic entity, but it is incompletely detached from the *Kewanius* lineage. These forms in the area of overlap exhibit features of both lines, whereas other forms in this area, for example *amplus*, *angularis*, *paroicus*, *crassatus*, and *simplex*, do not show characteristics of *birdi*. Consequently, the *birdi* and *Kewanius* lineages demonstrate the phenomenon labeled “incomplete synapomorphy” by Shelley and Whitehead (1986).

Another problematical species is *clavatus*, placed in the *melacis* lineage because of its small size and relatively unadorned aperture (Fig. 205). Geographically, the only other possibilities are the *varius* and *impurus* groups, *Kewanius* lineage, all of whose species possess either long acropodites or divided apertures with pouches and broadly terminal acropodites, respectively. Consequently, *clavatus* would disrupt the harmonies of these ensembles, but its narrowly terminal acropodites are also divergent from other forms of the *melacis* lineage, not to mention unique to the genus, since they arise from the outer, rather than the inner, prefemoral margins. The acropodite of *clavatus*, proportionately slightly longer than those of the other species of the *melacis* branch, may reflect genetic influence of the parapatric species, *impurus*, and may be an example

of "incomplete synapomorphy" between the *melacis* and *Kewanius* lineages.

Notwithstanding these questionable species, I think that the *impurus*, *varius*, *simplex*, and *dubius* groups unite to form a coherent ensemble, which is incompletely detached from the *birdi* branch. As stated earlier, these four groups are distinguished on the basis of acropodal features for convenience and to facilitate comprehension of the genus, but they are closely related and contain all forms with divided apertures and pouches, or with gonopods or apertures similar to such forms. For example, *goodi* lacks pouches, but its gonopods possess long acropodites similar to those of *angularis*, which has pouches. Conversely, *dubius*, parapatric to *goodi*, has upright telopodites with short, broadly terminal acropodites that are only very slightly curved, but its aperture is shared with *goodi*. I assigned *goodi* to the *impurus* group because of the long acropodite, which excludes *dubius*. Nor does *dubius* fit in the *varius* group, whose components display divided apertures with pouches, and variably curved to leaning telopodites. The only alternative for *dubius* is a separate species group, which is part of the parent lineage because of the shared aperture configuration with *goodi*.

Elsewhere, the *simplex* and *varius* groups blend together through *varius* itself, since *v. christianus*, with a distally lobed prefemur and a broadly terminal but sharply discontinuous acropodite, bridges the anatomical gap between the subterminal or narrowly terminal, and therefore discontinuous, acropodites of the former, and the smoothly continuous, poorly demarcated ones of the latter. Furthermore, *angularis*, with divided apertures and pouches, connects the *impurus* with the *simplex* and *varius* groups. The pouches alone suffice for this purpose, but their variability is an important additional factor. In some forms of *angularis*, the pouches are broad and open, thereby resembling the conditions in *paroicus* and *crassatus* of the *simplex* group (compare figs. 18 and 23 with figs. 123 and 127), whereas the pouches of other forms are narrow and closed, and thus more like the conditions in *amplus* and *varius* of the *varius* group (compare fig. 21 with figs. 64 and 73). Finally, *compressus*, with a moderately long acropodite, 3/8 of the telopodite length, blends the *impurus* and *varius* groups by bridging the anatomical gap between short and long acropodites,  $\leq 1/4$  and  $\geq 1/2$  of the telopodite length, respectively. Thus, differences between the *impurus*, *dubius*, *varius*, and *simplex* groups enable them to be distinguished for convenience, to simplify

*Eurymerodesmus*, but there are many unifying factors that merge them into a single lineage covering much of the generic range (Fig. 214, number 4). For ease of recognition this lineage is referenced by the older available genus-group name, *Kewanius*, since there is no single, representative species.

As stated previously, the *birdi* group connects with this ensemble through *polkensis*, *caesariatus*, *pulaski*, and *serratus*, and possibly also *goodi* and *dubius*, but otherwise it is detached and maintains a consistent and independent set of features in parts of Louisiana and Arkansas where they are sympatric. Consequently, I regard the *birdi* group as a separate lineage, loosely attached to, and sister to, the *Kewanius* line. With only one component species group and no available genus-group name, it is referenced as the *birdi* lineage.

The *melacis* group occupies a peripheral geographical position along the southern and western generic boundaries and is overlapped by the southern, finger-like extension of the *birdi* lineage and the allopatric populations of *amplus*, *varius* group, *Kewanius* lineage, to which it is otherwise parapatric (Fig. 213). There are no discernible anatomical similarities and no clear connections between the *melacis* group and the previous assemblages, the only possible exception being the slightly longer acropodite of *clavatus* that may reflect influence of *impurus*. The generally upright, sublinear telopodites of *digitatus* are phenotypically similar to, and convergent with, those of *dubius*, some 240 miles to the east. Likewise, the phenotypically similar, dactyliform cyphopodal projections of *dactylocyphus* and *compressus* are structurally different and reflect convergence. Consequently, the *melacis* group clearly represents a separate assemblage, which is referenced as the *melacis* lineage since there is no available genus-group name. Because of its generally peripheral position (Fig. 214, number 1) and the absences of both pouches and true lobes on the apertures, I consider the *melacis* lineage to be sister to the rest of the genus and family (Fig. 215). It is the least differentiated and apparently most plesiomorphic ensemble.

With only one species and two widely allopatric samples, the *hispidipes* group cannot be treated in detail. The Coles County, Illinois, site is peripheral and allopatric to the rest of the generic range, whereas the southern Arkansas locality is in the area of greatest species diversity and sympatric with both the *impurus* and *varius* groups, *Kewanius* lineage (Fig. 213). There are no unequivocal anatomical similarities with other lineages, but I detect a slight



suggestion of a distal prefemoral swelling, possibly indicating affinity with the *simplex* group, *Kewanius* lineage. Because it cannot be linked to another species, *hispidipes* comprises a separate species group and lineage whose phylogenetic position is determined by default, since the positions of the other lineages can be logically inferred (Fig. 215). However, there are also geographical and anatomical grounds for this placement, since its sympatry and the aforementioned anatomical similarity suggest closer affinity to the *birdi* and *Kewanius* lineages than is shown by the *melacis* branch. The genus-group name *Eurymerodesmus*, the oldest one in the family, is available for this line, but I hesitate to employ this name below the generic level without being certain of its usage. Future material may provide the necessary evidence to merge *hispidipes* with either the *birdi* or *Kewanius* lineages, thus clearly comprising a *Eurymerodesmus* branch. This is currently impossible, and hence, it is referenced as the *hispidipes* line.

Like *Sigmoria* in the east, *Eurymerodesmus* is a giant mosaic complex that blankets much of the southeastern and south-central United States (Figs. 1, 213-214). We are seeing this assemblage near its zenith, near maximal expansion with minimal extinction, before major anatomical and geographical discontinuities develop. It consists of four lineages or major components that overlie each other to varying degrees (Fig. 214), but since the *hispidipes* branch contains only one species, for practical purposes there are only three such ensembles. The *Kewanius* branch covers the southeastern and south-central areas and is overlapped in the western third of its range by the incompletely detached *birdi* lineage; the *melacis* line occupies the southwestern corner of the range, where it is largely independent from, and only minimally overlapped by, the other two components. Thus, the *birdi* branch is partly superimposed on both the *Kewanius* and *melacis* lineages, which are essentially parapatric (Fig. 214). Previous workers have merely extracted forms from various parts of these lineages and, because they display different combinations of the features of the apertures and gonopods, assumed that they represent distinct species and assigned new names at this taxonomic level. Not having personally collected *Eurymerodesmus* to the extent that I did *Sigmoria*, I cannot personally attest to the degree of partitioning, nor can I detail the extent to which clinal gradients traverse the range without much more material, particularly in the *Kewanius* lineage. However, the apertures and gonopods are independent of each other in

the *simplex* group, reflecting influence of the incompletely detached *birdi* lineage. As the acropodite progresses from narrowly terminal to subterminal, the aperture changes from divided with pouches in *simplex*, to undivided with sizeable caudal lobes in *polkensis* and indistinct elevations in *caesariatus*, returns to divided with pouches in *paroicus* and *crassatus*, and is undivided with moderate lobes in *pulaski* and *serratus*. Trends in these two features therefore run counter to each other, but the full extent of this phenomenon is unknown.

In *Sigmoria*, Shelley and Whitehead (1986) defined species as taxa that appear segregated from geographically proximate taxa and are not connected by intergrades, hence seemingly reproductively isolated. Evidence for isolation included syntopy between phenotypically distinct forms, range disjunctions between taxa that could otherwise be considered subspecies, and abrupt range discontinuities between proximate forms, resulting in tightly fitted parapatry patterns. Subspecies were defined as reasonably homogeneous taxa that are continuous with other such taxa through intergrade or intermediate forms. I have attempted to apply these definitions to *Eurymerodesmus*, but the nature of the interfaces between forms can rarely be determined because of incomplete material. Thus, forms that appear to be parapatric and hence are considered species in this first revision may eventually need to be reevaluated. Beyond this procedural difficulty, there are interpretation problems in the *Kewanius* lineage that hinder taxonomic decisions. For example in the *impurus* group, I lumped dissimilar variants together under *angularis* but retained *compressus*, in the middle of this area, as a valid species. Though seemingly inconsistent, I think that the anatomical differences in both sexes of *compressus* (shorter acropodite, longer and dissimilar cyphopodal projections) warrant taxonomic recognition. Other interpretations of this situation are possible, and the question arises as to whether *compressus* really is reproductively isolated or a highly localized, point-form variant of *angularis*. Perhaps *compressus* actually represents a combination of stages in clinal trends in the aperture and gonopods that produce a variant of such phenotypic distinctiveness as to appear reproductively isolated when it actually is not. Similarly in the *varius* group, I combined variants of *amplus* but maintained taxonomic distinction from *varius*, although some forms of *amplus* and *v. louisianae* with intermediate densities of prefemoral hairs appear to bridge the anatomical gap between the species.

The picture is clearer in the *melacis* lineage because there is less interference from overlapping branches and because of less inherent intricacy. Relatively extensive collecting has also taken place along the interfaces between *melacis*, *dactylocyphus*, and *digitatus*, disclosing tightly fitted parapatric spatial relationships with minimal overlap (Fig. 176). Consequently, this situation exhibits abrupt range discontinuities, which are prevalent in *Sigmoria* and interpreted as evidence for reproductive isolation. Slight differences between *digitatus* and *sanbernardiensis*, chiefly involving the orientation of the acropodite, suggest that they may be forms of a single species, but more material is needed from intervening areas in Fayette, Bastrop, Lee, and Williamson counties. As in the *Kewanius* lineage, the question also arises as to whether the parapatric forms really are reproductively isolated and hence full species.

Thus as stated in the introduction, a question that must be posed at the conclusion of this study is whether the parapatric "species" of *Eurymerodesmus* and *Sigmoria* really are true species, reproductively isolated from each other. They facilitate comprehension of the mosaics but may be more on the order of semispecies. Perhaps the parent major components in *Sigmoria*, which demonstrate properties of species (Shelley and Whitehead 1986), and the lineages in *Eurymerodesmus* should be viewed as superspecies and hence the functional species. However, semispecies and superspecies lack nomenclatorial status and cannot be recognized taxonomically, so it is convenient to continue the practice of recognizing the localized, primarily parapatric entities at the species level, particularly since many have already been named by past authors.

The present contribution therefore applies the species category to two markedly dissimilar entities that logically should be discriminated. *Eurymerodesmus birdi* and *mundus* are broadly sympatric over a large area, unquestionably reproductively isolated, and hence unequivocal species. *Eurymerodesmus hispidipes*, with two small, widely allopatric populations, may also be such but is too poorly known to determine now. The "species" in the *Kewanius* and *melacis* lineages, however, are chiefly localized with varying degrees of differentiation. Sympatry, when it occurs, is mostly restricted to narrow zones at interfaces. Hence, the latter entities are not equivalent to *birdi* and *mundus*, so perhaps the true species in the *Kewanius* and *melacis* lineages are the lineages themselves. Consequently, a more theoretically sound view of *Eurymerodesmus* may be

that it contains only five component species. This decision and the companion theoretical considerations are left to future workers.

#### CONCLUSION

Diplopodological research lags far behind that on other animals, even other arthropods, despite the impressive research potential of millipeds. Hoffman (1969, 1985) equated the state of the art with those of entomology and ornithology in the early 1800's and estimated (1985) that only about 20% of the global fauna had been described. This percentage extrapolates to around 50,000 "species" on the planet, quite possibly a conservative estimate. The prospects for the future become gloomy when it is noted that less than a dozen systematic specialists exist to investigate this large class (Hoffman 1985), with only three in the entire Western Hemisphere, all in the eastern United States. Moreover, several of the more productive and broadly-based students are at or near the ends of their careers, and few newcomers are entering the field. As currently practiced, diplopodology competes poorly with more glamorous disciplines of modern biology and may become even more neglected in the next 25-50 years, when the youngest present investigators retire. I therefore think that prudence requires a different slant to taxonomic research, that it should be directed more towards integrating knowledge throughout the class than towards the intricacies of single taxa. There are far more nomenclatorial tangles and unrevised genera than the few of us can ever clarify, and we can describe new forms indefinitely without beginning to impact on the global fauna. A major objective of scientific research is the drawing of generalities from cumulative individual observations, and if this is ever to happen with millipeds, it must be now while a number of knowledgeable investigators is still alive and productive. Consequently, it is timely to expand beyond purely descriptive and revisionistic taxonomy by evaluating the knowledge from such studies for possible insights into the Diplopoda as a whole. Common patterns, shared by many taxa, may hold broad evolutionary implications for the class, but these patterns must first be identified.

With revisions of two speciose mosaic complexes now complete, those of *Sigmoria* (Shelley 1981, Shelley and Whitehead 1986) and *Eurymerodesmus*, the questions arise as to how widespread the phenomenon is and whether it holds general principles for these poorly agile arthropods. Shelley and



Whitehead (1986) noted that problem groups, in which species and genera are difficult to delineate, exist throughout the class and suggested the following as examples of potential mosaics: *Rhysodesmus*, *Nannaria*, and the California representatives of the tribe Xystocheirini (*Xystocheir*, *Paimokia*, *Ampliocheir*, and *Motyxia*) (Polydesmida: Xystodesmidae); *Amplinus* and *Pycnotropis* (Polydesmida: Platyrrhacidae); *Chondrodesmus* (Polydesmida: Chelodesmidae); and the family Rhinocricidae (Spirobolida). I have subsequently scoured the modern literature for evidence of additional complexes and suggested (1989) unspecified genera in the following families: Glomeridesmidae (Glomeridesmida); Spirobolellidae and Pachybolidae (Spirobolida); Spirostreptidae, Cambalopsidae, and Pseudonannolenidae (Spirostreptida); Conotylidae and Clei-

dogonidae (Chordeumatida); and Paradoxosomatidae, Chelodesmidae, Platyrrhacidae, Oxydesmidae, Xystodesmidae, Sphaeridesmidae, Polydesmidae, Fuhrmannodesmidae, Pyrgodesmidae, and Dalodesmidae (Polydesmida). I now augment this roster by listing (Table 8) all milliped genera with 10 or more known or suspected species according to Hoffman (1979); those with 20 or more congeners are denoted by asterisks. Most of these taxa have not received comprehensive or even cursory modern study and cannot be reviewed. However, the literature of many that have been investigated contains evidence of similarities to *Sigmoria* and *Eurymerodesmus*, suggesting comparable underlying phenomena. Consequently, these and unstudied genera in table 8 may be additional, but currently undetected, mosaics.

Table 8. Speciose Milliped Genera (10 or more species) (Hoffman 1979)

\*taxa with  $\geq 20$  species

PENICILLATA	Rhinocricidae	* <i>Prionopetalum</i> - 21
POLYXENIDA	* <i>Eurhinocricus</i> - numerous	<i>Rhamphidaropoides</i> - 15
Polyxenidae	* <i>Salpidobolus</i> - numerous	* <i>Spinotarsus</i> - about 96
<i>Polyxenus</i> - about 10 species	Pachybolidae	<i>Syndesmogenus</i> - 13
Lophoproctidae	<i>Aulacobolus</i> - about 12	<i>Tibiomus</i> - 10
<i>Lophoturus</i> - about 15	* <i>Centrobolus</i> - about 44	JULIDA
PENTAZONIA	<i>Eucarla</i> - about 10	Julidae
GLOMERIDESMIDA	SPIROSTREPTIDA	<i>Julus</i> - 13
Glomeridesmidae	Cambalidae	<i>Ophiulius</i> - 18
* <i>Glomeridesmus</i> - 23	* <i>Nannolene</i> - about 22	* <i>Leptoiulus</i> - numerous
SPHAEROTHERIIDA	Cambalopsidae	<i>Xestoiulus</i> - about 16
Sphaerotheriidae	* <i>Trachyjulus</i> - about 23	* <i>Allajulus</i> - numerous
* <i>Sphaerotherium</i> - about 50	<i>Hypocambala</i> - about 10	<i>Typloiulus</i> - 17
<i>Cyliosoma</i> - about 10	Iulomorphidae	* <i>Amblyiulus</i> - numerous
Sphaeropoecidae	<i>Iulomorpha</i> - about 14	<i>Dolichoiulus</i> - 19
<i>Sphaeropoecus</i> - about 12	Pseudonannolenidae	<i>Mesoiulus</i> - about 10
* <i>Castanotherium</i> - about 20	* <i>Pseudonannolene</i> - about 30	<i>Pachyiulus</i> - about 15
GLOMERIDA	* <i>Epinannolene</i> - about 25	* <i>Anaulaciulus</i> - about 30
Glomeridae	Spirostreptidae	* <i>Megaphyllum</i> - numerous
* <i>Glomeris</i> - about 80	<i>Alloporus</i> - about 17	* <i>Ommatoiulus</i> - numerous
Trachysphaeridae	<i>Archispirostreptus</i> — about 15	Parajulidae
* <i>Trachysphaera</i> - about 30	<i>Gymnostreptus</i> - about 17	<i>Aniulus</i> - about 17
HELMINTHOMORPHA	* <i>Orthoporus</i> - about 40	<i>Bollmaniulus</i> - about 12
POLYZONIIDA	<i>Plusioporus</i> - about 13	<i>Oriulus</i> - about 10
Polyzoniida	<i>Urostreptus</i> - 11	<i>Parajulus</i> - about 15
<i>Polyzonium</i> - about 11	<i>Trienostreptus</i> - 10	Mongoliulidae
STEMMIULIDA	Harpagophoridae	<i>Skleroprotopus</i> - 14
Stemmiulidae	<i>Zinophora</i> - about 16	Paeromopodidae
* <i>Diopsiulus</i> - 37	<i>Gonoplectus</i> - 19	<i>Californiulus</i> - 10
* <i>Prostemmiulus</i> - about 42	<i>Thyropygus</i> - about 18	Blaniulidae
* <i>Stemmiulus</i> - 20	<i>Remulopygus</i> - about 10	<i>Blaniulus</i> - about 10
SPIROBOLIDA	<i>Spissustreptus</i> - 10	<i>Nopoiulus</i> - 10
Messicobolidae	Odontopygidae	SIPHONOPHORIDA
<i>Messicobolus</i> - 14	* <i>Peridontopyge</i> - about 30	Siphonophoridae
Atopetholidae	<i>Chaleponcus</i> - 19	* <i>Siphonophora</i> - uncertain
<i>Arinolus</i> - 11	<i>Helicochetus</i> - 13	PLATYDESMIDA
Spirobolellidae	<i>Kompsoprium</i> - 12	Platydesmidae
* <i>Spirobolellus</i> - about 80	<i>Patinatius</i> - 13	* <i>Platydesmus</i> - 27

To document the evidence for mosaics for specific genera in table 8 would be prohibitively long (general clues to mosaics are detailed briefly in the appendix), but the undeniable literature pattern must be acknowledged. To varying degrees throughout the Diplopoda there are statements and characterizations in publications on speciose genera resembling ones made years ago about *Sigmoria* and *Eurymerodesmus*, suggesting that these genera are other mosaic assemblages. The cumulative weight of this evidence implies that mosaic complexes are a major evolutionary phenomenon warranting serious consideration by diplopodologists. I focus here on large, speciose mosaics because their literature clues are easier to detect, but smaller, less diverse taxa can also constitute mosaics, for example the xystodesmid genus *Dicellarius*, with five species and five subspecies (Shelley 1984c). Since they are less intricate and their literature is comparatively straightforward, small mosaics are easier to grasp. They do not generate the massive confusion of large mosaics

covering sizeable parts of one or more continents, so for the purposes of this contribution, table 8 is restricted to genera with 10 or more species according to Hoffman (1979). There are undoubtedly other speciose genera currently with less than 10 known species, for example *Striaria* (Chordeumatida: Striariidae), widespread in eastern and western North America. My purpose here is not to state absolutes but to alert diplopodologists to a widespread phenomenon and to encourage searching beyond parochial taxonomic and faunal interests for general underlying principles while there are still enough broadly-based workers to do so. We will never know the full intricacies of such widely-ranging genera as *Barydesmus*, *Chondrodesmus*, *Mestosoma*, *Orthoporus*, *Eurhinocricus*, and *Spirobolellus*; the necessary levels of field sampling are not currently possible, and many forms are probably becoming extinct through deforestation and habitat loss. However, diplopodologists can still attempt to infer common properties and

Table 8. (Continued)

CALLIPODIDA		
Schizopetalidae		
<i>Acanthopetalum</i> - 15		
<i>Eurygyrus</i> - about 14		
<i>Apfelbeckia</i> - about 10		
CHORDEUMATIDA		
Conotylidae		
<i>Conotyla</i> - 13		
<i>Taiyutyla</i> - 14		
Mastigophorophyllidae		
<i>Mastigophorophyllon</i> - about 13		
Haaseidae		
<i>Haasea</i> - about 14		
Cleidogonidae		
* <i>Pseudotremia</i> - about 25		
* <i>Cleidogona</i> - about 74		
Trichopetalidae		
<i>Trichopetalum</i> - about 10		
Craspedosomatidae		
<i>Craspedosoma</i> - about 10		
* <i>Pyrgocyphosoma</i> - about 28		
* <i>Ochogona</i> - uncertain		
Chordeumatidae		
<i>Chordeuma</i> - about 12		
Anthroleucosomatidae		
<i>Anamastigona</i> - about 12		
<i>Brachychaeteuma</i> - 10		
Caseyidae		
* <i>Caseya</i> - 21		
<i>Opiona</i> - 13		
POLYDESMIDA		
Paradoxosomatidae		
<i>Aulacoporus</i> - 10		
<i>Aschistodesmus</i> - 15		
<i>Eviulisoma</i> - 15		
	* <i>Scolodesmus</i> - 20	
	<i>Eustrongylosma</i> - 15	
	<i>Antheromorpha</i> - 12	
	<i>Orthomorpha</i> - 17	
	<i>Tectoporus</i> - 14	
	<i>Xanthodesmus</i> - 14	
	<i>Stosatea</i> - about 14	
	<i>Catharosoma</i> - 13	
	* <i>Mestosoma</i> - about 50	
	Chelodesmidae	
	<i>Eurydesmus</i> - about 17	
	* <i>Leptodesmus</i> - 21	
	<i>Biporodesmus</i> - 10	
	* <i>Trichomorpha</i> - about 35	
	* <i>Chondrodesmus</i> - about 40	
	<i>Brasilodesmus</i> - 11	
	<i>Caraibodesmus</i> - 10	
	<i>Strongylomorpha</i> - about 10	
	<i>Paracordyloporus</i> - about 15	
	* <i>Amphelictogon</i> - 22	
	<i>Sandalodesmus</i> - 13	
	Xystodesmidae	
	* <i>Xystocheir</i> ( <i>Paimokia</i> , <i>Amplocheir</i> , <i>Motyxia</i> ) - uncertain	
	* <i>Riukiaria</i> - about 20	
	* <i>Rhysodesmus</i> - about 70	
	<i>Stenodesmus</i> - 10	
	* <i>Brachoria</i> - about 28	
	* <i>Sigmoria</i> - 65	
	* <i>Nannaria</i> - about 28	
	<i>Parafontaria</i> - about 16	
	Eurymerodesmidae	
	* <i>Eurymerodesmus</i> - 25	
	Gomphodesmidae	
	* <i>Uloidesmus</i> - about 20	
	Oxydesmidae	
	* <i>Coromus</i> - numerous	
	<i>Lyodesmus</i> - about 13	
	Sphaeriodesmidae	
	* <i>Sphaeriodesmus</i> - 21	
	Platyrrhacidae	
	* <i>Platyrrhacus</i> - numerous	
	* <i>Barydesmus</i> - numerous	
	* <i>Psammodesmus</i> - numerous	
	* <i>Aphelidesmus</i> - about 28	
	* <i>Amplinus</i> - about 28	
	<i>Pycnotropis</i> - about 15	
	Rhacodesmidae	
	<i>Aceratophallus</i> - 12	
	Polydesmidae	
	* <i>Epanerchodus</i> - numerous	
	* <i>Polydesmus</i> - numerous	
	<i>Pseudopolydesmus</i> - about 13	
	<i>Scytonotus</i> - about 11	
	Cryptodesmidae	
	<i>Apomus</i> - 12	
	<i>Peridontodesmus</i> - about 11	
	* <i>Aporodesmus</i> - about 25	
	Nearctodesmidae	
	<i>Nearctodesmus</i> - about 13	
	Pyrgodesmidae	
	<i>Calymmodesmus</i> - about 16	
	<i>Docodesmus</i> - about 14	
	Cyrtodesmidae	
	* <i>Cyrtodesmus</i> - about 25	
	Dalodesmidae	
	<i>Anaulacodesmus</i> - 16	
	* <i>Icosidesmus</i> - about 38	
	<i>Dityloura</i> - 12	
	* <i>Vanhoeffenia</i> - about 70	



mechanisms, and search with open minds for basic truths applicable to the broad spectrum of the class.

Interpretation of mosaic complexes is beyond the scope of this work, but the phenomenon raises many intriguing questions. Why do so many millipeds form these assemblages, and how does this process occur? Is the phenomenon applicable to any genus? When we name and describe "species" in mosaics, are we really characterizing species or lesser entities, perhaps semispecies? As may be the case with the *Kewanius* and *melacis* lineages of *Eurymerodesmus*, do some of our proposed species groups and possibly even genera instead constitute species, thus implying that higher hierarchical levels may need to be lowered? Do mosaic complexes hold clues or explanations for other phenomena? Since partitioning coupled with extinctions isolated the highly atypical forms in the southern periphery of *Sigmoria*, could this general process explain the origins of such enigmatic geographical oddities as *Choctella* (Spirostreptida: Pseudonannolenidae) (Shelley 1989)? Could it be the former northern component of an ancient pseudonannolenid mosaic that is so anatomically dissimilar as to have appeared to require a monotypic family (Chamberlin and Hoffman 1950; Hoffman 1969, 1979) and is now so isolated as to be the only remaining Nearctic representative? Does much of today's global diplopod picture reflect stages in the formation and breakdown of mosaics, with some genera in expansion phases, others, like *Sigmoria* and *Eurymerodesmus*, near their zeniths, and still others in periods of decline, with significant anatomical and geographical discontinuities resulting from extinctions? As suggested by Shelley and Whitehead (1986) does this phenomenon in millipeds mirror ones in other poorly vagile organisms, for example certain soil insects, arachnids, and possibly even other myriapods, and could diplopods become something of a model for investigating it? Perhaps the road to significantly advancing diplopodology and attracting more students is not through classical revisions and faunistic treatments, though these are necessary, but through the entirely different route of investigations on shared *phenomena*, common to many taxa. Perhaps the few current diplopodologists, in an effort to salvage the field and heighten its appeal to outside specialists and potential new students, should concentrate more on dynamic processes and less on static descriptions, in essence focusing on what millipeds *do* instead of what they are. The dynamics of mosaic complexes seems a promising arena for future investigations that may significantly enhance

our understanding of milliped evolution. With a diminishing number of specialists and a correspondingly bleak outlook, the time to pursue it is now.

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## APPENDIX

## Literature Clues to Speciose Mosaic Complexes in the Diplopoda

1. Restricted component distributions.
2. Parapatry of relatively localized components as revealed by distribution maps like that of *Eurymerodesmus* species in Texas (Fig. 212).
3. Statements about small or minor differences between species.
4. Uncertainty, confusion, and/or contradictions and disagreements among authors, particularly concerning the composition, generic positions, or taxonomic statuses of species groups.

Variations of general anatomical (usually gonopodal) patterns, like those shown by the subgenera of *Sigmoria* and the lineages of *Eurymerodesmus*, are subject to different interpretations by different authors, or the same author at different stages, which in turn lead to conflicting published opinions about generic validities, synonymies, and group compositions. When several such opinions are published, as with genera in the tribe Amplinini (Polydesmida: Platyrrhacidae), a highly confused literature results, with contradictions and disagreements similar to those in *Eurymerodesmus* and *Sigmoria* before they were revised. Thus, muddled literature, a reflection of inherent intricacy, is a particularly telling clue to a potential mosaic.

A common thread in the literature of speciose genera are statements about small or minor differences between species, for example as between *melacis/sanbernardiensis/digitatus* and *elevatus/newtonus/amplus/variatus* in *Eurymerodesmus* and between congeners in all subgenera of *Sigmoria* (Shelley 1981, Shelley and Whitehead 1986). In the latter genus, contiguous populations of adjacent species are often phenotypically similar because of residual ancestral character clines traversing the boundaries. Hence it was difficult to formulate definitions of many species that excluded neighboring populations of others, and initially, virtually every sample in parts of the range appeared to represent a separate species. Likewise in *Eurymerodesmus*, species definitions are difficult in the *Kewanius* and *melacis* lineages. Consequently, statements about slight differences between species in other genera probably reflect the effects of a mosaic, which should be expected when a genus appears to contain an inordinate number of species.

## INDEX TO TAXA

Synonyms in *italics*, new species in **boldface**

- amplus*, *Eurymerodesmus* — 45  
*angularis*, *Eurymerodesmus* — 31  
*bentonus*, *Eurymerodesmus* — 53  
*birdi*, *Eurymerodesmus* — 72, 74  
*birdi birdi*, *Eurymerodesmus* — 74  
*birdi planus*, *Eurymerodesmus* — 77  
*booneus*, *Eurymerodesmus* — 7  
**caesariatus**, *Eurymerodesmus* — 64  
*christianus*, *Eurymerodesmus* — 46  
**clavatus**, *Eurymerodesmus* — 94  
*columbus*, *Paresmus* — 38  
*compressus*, *Eurymerodesmus* — 35  
**crassatus**, *Eurymerodesmus* — 66  
*creolus*, *Eurymerodesmus* — 74  
**dactylocyphus**, *Eurymerodesmus* — 87  
*digitatus*, *Eurymerodesmus* — 91  
*dubius*, *Eurymerodesmus* — 38  
**elevatus**, *Eurymerodesmus* — 59  
*Eurymerodesmidae* — 18  
*Eurymerodesmus* — 19  
*evides*, *Auturus* — 7  
*floridus*, *Leptodesmus* — 78  
*goodi*, *Eurymerodesmus* — 36  
*hamatilis*, *Eurymerodesmus* — 49  
*hispidipes*, *Eurymerodesmus* — 25, 49, 55  
*hispidipes*, *Leptodesmus* — 25, 49, 68, 69, 74, 78  
*hispidipes*, *Polydesmus* (*Paradesmus*) — 25  
*hispidipes*, *Polydesmus* (*Polydesmus*) — 25  
*impurus*, *Eurymerodesmus* — 29  
*impurus*, *Leptodesmus* — 29  
*impurus*, *Paresmus* — 29  
*impurus*, *Polydesmus* — 29  
*Kewanius* — 19  
*louisianae*, *Eurymerodesmus* — 47  
*melacis*, *Eurymerodesmus* — 82  
*minimus*, *Eurymerodesmus* — 43  
*mundus*, *Eurymerodesmus* — 78  
*newtonus*, *Eurymerodesmus* — 53  
*oliphantus*, *Eurymerodesmus* — 55  
*Paresmus* — 19  
*paroicus*, *Eurymerodesmus* — 65  
*paroicus*, *Paresmus* — 65  
*planus*, *Eurymerodesmus* — 77  
*plishneri*, *Eurymerodesmus* — 74  
*polkensis*, *Eurymerodesmus* — 62  
*polkensis*, *Paresmus* — 62  
*pulaski*, *Eurymerodesmus* — 68  
*pulaski*, *Paresmus* — 68  
*sanbernardiensis*, *Eurymerodesmus* — 90  
*schmidtj*, *Eurymerodesmus* — 74  
**serratus**, *Eurymerodesmus* — 69  
*simplex*, *Eurymerodesmus* — 60  
*simplex*, *Kewanius* — 60  
*spectabilis*, *Eurymerodesmus* — 47  
*varius*, *Eurymerodesmus* — 41, 43  
*varius*, *Leptodesmus* — 43  
*varius*, *Polydesmus* — 43  
*varius christianus*, *Eurymerodesmus* — 46  
*varius louisianae*, *Eurymerodesmus* — 47  
*varius varius*, *Eurymerodesmus* — 43  
*wellesleybentoni*, *Eurymerodesmus* — 31  
*wellesleybentonus*, *Eurymerodesmus* — 31